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A thesis submitted in fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Anthropology

Durham University

2019

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This dissertation reports on the palaeoenvironmental reconstructions of several Pleistocene sites from Java (mainly Trinil, Kedung Brubus and Sangiran), based on newly developed ecomorphological methods for the cervid calcaneus and intermediate phalanx. Using a geometric morphometrics approach, 3D-landmark data were collected on extant cervids of known habitat preference, to establish correlations between morphological traits, locomotor behaviour and environmental parameters. These models were then applied to deer fossils from the selected sites to assess past vegetation structure and substrate type.

This study extends the suite of ecomorphological methods available for palaeoenvironmental reconstruction. The morphology of the calcaneus and intermediate phalanx were found to vary with locomotor strategy and habitat along a continuum from open habitats with dry substrate to closed habitats with wet substrate. Furthermore, this dissertation contributes to our understanding of the understudied Pleistocene environments of Java. The results of Trinil confirmed interpretations of an open woodland, but suggested a relatively wet substrate. The results of Kedung Brubus and its associated fauna indicated open, but drier conditions and presumably coincided with a glacial stage when Java was connected to the Asian mainland, allowing increased biotic interchange with the continent. The material from Sangiran suggested open conditions, and either dry or wet substrates, possibly reflecting the mixed nature of the assemblage.

The early dispersal of *Homo erectus*, considered the first hominin to have expanded its biogeographic range over large parts of the Old World, is generally hypothesized to have been more driven by either extrinsic (e.g. the expansion of open environments) or intrinsic factors (e.g. the increased capacity of *H. erectus* to adapt to variable conditions). The reported palaeoenvironmental reconstructions provide an estimate of the extent to which this species depended on a specific type of environment. The results do not contradict a scenario where *Homo erectus* was restricted to more open environments for its survival and dispersal. A significant degree of environmental flexibility can, nevertheless, be extrapolated from its presence in dry and wet conditions, and in areas with different vegetation structures ranging from grassland to open woodland.

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List of abbreviations

AMNH= American Museum of Natural History, New York, U.S.

ANOVA= Analysis of Variance

ASM= Anatomische Staatssamlung München, Germany

bg-PCA= between groups Principal Component Analysis

CAR= Center for Artefact Research vzw, Mechelen. Belgium

cc= cubic centimetre

CMC= Canadian Museum of History, Gatineau, Canada

Fig.= Figure

GMM= Geometric Morphometrics

GPA= Generalized Procrustes Analysis

H.K.= Haupt-Knochen Schicht (main fossiliferous layer)

IMNH= Idaho Museum of Natural History, Pocatello, U.S.

ITCZ= Intertropical Convergence Zone

Ka= Thousand years ago

Km= Kilometer

KBIN= Royal Belgian Institute of Natural Sciences, Brussels, Belgium

LDA= Linear Discriminant Analysis

Ma= Million years ago

MANOVA= Multivariate Analysis of Variance

MFN= Museum für Naturkunde, Berlin, Germany

mm= milimeter

MNHN= National Museum of Natural History, Paris, France

MPIEVA= Max Plack Institute of Evolutionary Anthropology, Leipzig, Germany

N= Number

NISP=Number of Identified Specimens

NMR= Natural History Museum Rotterdam, The Netherlands

NPMANOVA= Non parametric Multivariate Analysis of Variance

p= calculated probability value

PC= Principal Component

PCA= Principal Component Analysis

Persbodibratlund= Personal collection Bodi Bratlund, Sweden

PGLS= Phylogenetic Generalized Least Squares analysis

R= Coefficient of correlation

R^2= Coefficient of determination

s.l.= Sensu lato

s.s.= Sensu stricto

RMNH= Naturalis Biodiversity Center, Leiden, The Netherlands

UL= University of Liège (Palaeontology Service), Belgium

ULILLE= University Charles-de-Gaule Lille III (Zooarchaeology lab), Lille, France

USNM= National Museum of Natural History, Washington D.C., U.S.

UWBM= University of Washington Burke Museum, Seattle, U.S.

WWII= World War II

Statement of copyright

Acknowledgements

"Make haste, my beloved, and be thou like to a roe or to a young hart upon the mountain of spices."

(King James Bible, Song of Solomon 8:14)

It is with pleasure that I thank the people who directly or indirectly contributed to the completion of this dissertation. Only with the help of a great number of individuals and institutions was it possible to bring this project to fruition.

First of all, I am greatly indebted to my supervisors. I cannot overstate my gratitude to Dr. Kris Kovarovic for providing me with the opportunity to embark upon this journey and for being such an inspiring mentor. Her insights, encouragement and unwavering support over the years have been instrumental to this research project. In addition to providing a welcoming atmosphere in Durham I will also not forget the hospitality I received from her and her family, having been invited to their lovely home in the countryside. I would also like to express my sincere gratitude to Prof. Sarah Elton, whom was always ready with advice and was there to provide support at times when I most needed it. I wish to thank her for her guidance, her thoroughness and her confidence in me.

Furthermore, I owe thanks to a number of people who have advised me on crucial points in this project, who have encouraged me to persevere and have provided guidance pertaining the technical and theoretical aspects of this dissertation. In this context, my gratitude goes to Dr. John de Vos for his advice, his encouragement and for introducing me to the world of Southeast Asian Pleistocene vertebrates. To Dr. Una-Strand Vidarsdottir I am grateful for taking the time to familiarize me with the technicalities of Geometric Morphometrics and for taking me under her wings during the early stages of the project. A special thank you goes to Dr. Tarek Oueslati for sharing with me his knowledge of vertebrate osteology, for the useful

discussions and for allowing me to work in his lab during the time I was finishing my dissertation.

I am grateful to Dr. Sabrina Curran and Dr. Robert Scott for answering my questions pertaining artiodactyl ecomorphology and phylogeny, to Dr. Andrea Cardini, Dr. Charlotte King and Dr. Catherine Cronier for discussions about morphometrics and to Dr. Christine Hertler, Dr. Anne-Marie Bacon, Dr. Stéphane Frère, Dr. Martin Pickford and Dr. Valérie Zeitoun for their advice concerning Southeast Asian fossil cervids. I thank Prof. Erik Catrysse for giving me the chance to sharpen my knowledge of gross anatomy in the dissecting room of the VUB and Prof. Dirk Verschuren for giving me the opportunity to gain experience with East African Quaternary palaeoecology as well. To Yvonne de Rue and Dana Piessens I am indebted for their flexibility and confidence to let me combine my research with various zooarchaeological projects in Mechelen. The Department of Anthropology (Durham University) is warmly thanked for the financial and logistical support that went into this project.

This dissertation would not have been possible without the support of a number of institutions and museum curators that provided me with access to their collections. I thank the following people for assisting me with access to materials: Reinier van Zelst, Natasha den Ouden and Pepijn Kamminga at the Naturalis Biodiversity Center, Dr. Valentin Fisher and Dr. Julien Denayer at the Palaeontology Service of the University of Liège, Henry van der Es of the Natural History Museum Rotterdam, Dr. Joséphine Lesur at the National Museum of Natural History (Paris), Dr. George Lenglet and Sebastien Bruaux at the Royal Belgian Institute of Natural Sciences (Brussels) and Thomas Schossleitner at the Museum für Naturkunde (Berlin). I am obliged to Dr. Jason Nadell, Dr. Briana Pobiner and Bobby Kaplan for helping me with scans from the American Museum of Natural History (New York) and the National Museum of Natural History (Washington D.C.). Special mention goes out to Dr. Erick

Setiyabudi and the rest of the team at the Geological Museum of Bandung (Indonesia) for their warm welcome and for all the assistance I was offered there.

Finally, I wish to express my gratitude to the other PhD-students of my cohort -especially Elena- for their encouragement, their reassurances and in general for making my time in Durham more than enjoyable. And last but not least, I thank my parents and my aunts Jacqueline and Julienne for their constant support and encouragement throughout my education.

Dedication

This thesis is dedicated to Jacqueline Gruwier and Julienne Gruwier.

1. Introduction

1.1 General introduction

In palaeoanthropology it is currently recognized that in order to understand key events in human evolution, it is important to place them in an environmental context (Vrba 1995a, Reed 1997, Potts 1998). One such key event, that has been the subject of intense scientific debate, is the appearance and rapid dispersal of *Homo erectus* over large parts of the Old World (Larsen *et al*. 1998, Anton 2003, Anton *et al.* 2016). Even though the underlying processes behind this biogeographic expansion remain poorly understood, it is thought that certain ecological parameters during the Plio-Pleistocene played a role (Anton & Swisher 2004, Lahr 2010, Agusti & Lordkipanidze 2011, Carotenuto *et al.* 2016). A number of researchers have suggested that the large scale development of open, savannah-like environments across Africa and Asia facilitated this expansion, and have pointed out that early hominin dispersal out of Africa was part of a larger ecosystem expansion (Vrba 1996, Dennell & Roebroeks 2005, Dennell 2010). Others have minimized the direct role of extrinsic factors, and have proposed that intrinsic factors, such as the appearance of bipedalism or cranial encephalization, led to an increased capacity for ecological flexibility and drove early *Homo* dispersal (Potts 1998, Bobe & Behrensmeyer 2004, Carotenuto *et al.* 2016).

While intrinsic and extrinsic factors are not mutually exclusive, and may well have both contributed to the success of *Homo erectus* (Carotenuto *et al.* 2016), understanding how they articulated, requires a more intimate grasp of the environmental conditions that were encountered by this hominin during the Early and Middle Pleistocene. Such a palaeoenvironmental framework is already available to some extent, but data are unequally distributed in time and space and the results of different proxies are sometimes contradictory. One region that has been comparatively neglected from a palaeoecological perspective is

Southeast Asia. Java especially, despite its wealth of *Homo erectus* fossils (Simanjuntak 2001), has received far less attention than East Africa. Moreover, current interpretations about the nature of its palaeoenvironments are still a matter of debate (see section 3.5.2.3). Nevertheless, this island does not only represent an important region because of its rich fossil record, but also because of its geographical position at the margins of the currently known *Homo erectus* range (Anton 2003, Anton *et al.* 2016, but see section 3.2). These factors, alongside the large amounts of faunal remains associated with the Indonesian *Homo erectus* sites, make Java not only an ideal test case for assessing the nature and role of environmental conditions in an "Out of Africa" scenario, but also a priority region for further research in hominin palaeoecology.

It is by studying the palaeontological record that ancient environments can be reconstructed and inferences made about hominin behaviour and morphology (Vrba 1975, Weinand 2004, Andrews & Hixon 2014). Although no single proxy is capable of providing a complete picture of the ecological conditions at a site, one approach within palaeontology that has made considerable contributions to our understanding of hominin palaeoecology, is that of artiodactyl ecomorphology (e.g. Kappelman 1988, Kappelman *et al.* 1997, Vrba 1980, 1995b, 1999, Plummer & Bishop 1994, Degusta & Vrba 2003, Kovarovic & Andrews 2007, Plummer *et al*. 2008, Barr 2014a). This method works by examining the functional morphology of skeletal elements in a mammal group as it relates to certain ecological variables (Degusta & Vrba 2003, Andrews & Hixon 2014). By comparing morphological patterns in recent mammals with those observed in extinct species, inferences can be made about probable adaptations in fossils (Andrews & Hixon 2014). Although the ecomorphological method has limitations of its own, it also has important advantages, such as taxonomic non-dependence (see section 4.3), that make it a powerful addition to traditional palaeontological analyses.

There is a considerable body of research on African bovids wherein the effectiveness of the ecomorphological method is demonstrated for several postcranial elements (e.g. Vrba 1980, 1995b, 1999, Köhler 1993, Kappelman 1988, Kappelman *et al.* 1997, Plummer & Bishop 1994, Degusta & Vrba 2003, 2005a, 2005b, Scott 2004, Barr 2014a, Barr 2018). Nevertheless, this technique has not yet been extensively applied on European and Asian assemblages, where palaeontological sites often comprise large numbers of cervid remains (Curran 2009). In response to this shortcoming, the present study seeks to develop ecomorphological models for a number of cervid elements and apply them on a selection of Indonesian sites, to gain further insight into the environments that were present there during the Pleistocene. As such, this is the first study of its kind in Southeast Asia after Weinand's (2005) thesis on the bovid astragalus, and certainly the first to apply it on cervids in this region. Even though the main objective of this dissertation is to generate new palaeoenvironmental evidence for a number of sites, it also contributes to the field of hominin palaeoecology by extending the suite of methods available for palaeoenvironmental reconstruction. The ecomorphological models presented here are based on species that come from across the cervid range and can theoretically be applied on any Pleistocene assemblage with sufficient deer fossils.

More specifically, this thesis provides ecomorphological models for the cervid calcaneus and intermediate phalanx. These skeletal elements are useful in ecomorphological analyses as they represent important components of the locomotor apparatus, a part of the artiodactyl body that, in terms of morphology, is thought to be mainly constrained by environmental parameters such as substrate type and vegetation structure (Leinders 1979, Köhler 1993, Degusta & Vrba 2005a, Polly 2007, Curran 2009, 2012, Barr 2014a,2014b, 2015). As such, the fossil materials on which the predictive models are applied can be informative about the type of vegetation that was present and whether substrates were of a dry or wet nature in the past.

Furthermore, this thesis aims to improve the way ecomorphological analyses are currently conducted. An important aspect of this is that for both the intermediate phalanx and the calcaneus a detailed functional framework is proposed, an aspect of ecomorphology that has received little attention in earlier studies of artiodactyls. The morphology of a skeletal element can be driven by a complex combination of different factors, including function, phylogeny, body size and sexual dimorphism. Therefore, a number of functional hypotheses are developed and tested about specific morphological traits, to objectively assess to what extent they are driven by function as related to ecology. In this light, a number of confounding factors (i.e. size, sexual dimorphism and phylogeny) are accounted for and discussed in detail (see section 4.3).

Another novel aspect is the use of 3D Geometric Morphometrics (GMM) instead of the more commonly used linear measurements. GMM has not yet been extensively applied on artiodactyl post-cranial elements, but nevertheless has some advantages over traditional morphometrics. Besides the fact that shape can be studied more independently from size (Viscosi & Cardini 2011), GMM also allows for skeletal elements to be analyzed as whole units instead of a number of separate measurements that do not maintain the original geometry of the object (Zelditch *et al.* 2004). By applying this methodology on 3D surface scans taken of skeletal elements, it is possible to capture subtle shape differences that would have been obscured using a traditional morphometric approach. Besides the fact that the potential of this methodological approach has not yet been fully explored in non-primate ecomorphology, it is especially relevant in the case of deer, as they are morphologically conservative (Lister 1996) and shape differences between species are expected to be rather subtle.

The ultimate goal of this study is to apply the predictive models developed here on cervid material from a number of hominin localities from Java: principally Trinil, Kedung Brubus

and Sangiran. In doing so, context is provided to the dispersal and success of *Homo erectus* in Asia. By comparing palaeoenvironmental reconstructions of different *Homo erectus* sites, an estimate can be made of the adaptive flexibility of this hominin. If reconstructions point to a specific and uniform type of (dry, open) environment for the different localities, the data would suggest a scenario where extrinsic changes predominantly drove early hominin expansion. If palaeoenvironmental reconstructions are indicative of a range of different environments that *Homo erectus* occupied, the data would be more suggestive of a scenario where intrinsic changes made *Homo erectus* a more flexible species, less restricted by specific environmental conditions in its dispersal.

The fossil assemblages selected for this analysis are particularly useful for such a study, as they are thought to correspond with two Pleistocene faunal stages (the Trinil H.K. stage: aprox. 0.9 Ma, and the Kedung Brubus stage: 0.7-0.8 Ma), and presumably coincided with one or more glacial-interglacial cycles (van den Bergh *et al.* 2001, Musser 1982, Sondaar 1994, Meijaard 2003a). In fact there is some evidence that during the more recent Kedung Brubus stage Java underwent substantial climatic changes (Musser 1982, Sondaar 1994, Meijaard 2003a). The nature and significance of these purported changes and how they were expressed in the regional environment, nevertheless, remain poorly understood.

The cervid ecomorphological analyses provided in this study, contribute to a complete and integrated picture of the palaeoenvironmental conditions in Java and improve our understanding of how significant potential environmental changes were during times when *Homo erectus* occupied the region. As such it allows for a better insight into the behaviour and adaptive flexibility of this early member of our genus and ultimately into the origins of modern human behaviour, which is characterized by the capacity to cope with a broad range of environments (Potts 1998).

1.2 Structure of this dissertation

Following this introduction, this dissertation is composed of seven more chapters. In Chapter 2 background is provided, by discussing the environmental conditions currently present in Java and how biotic and abiotic factors have in the past shaped the character of the island. The second part of Chapter 2 reviews the palaeontological record of Java within its wider Southeast Asian context and provides an account of the history of palaeozoological research in this part of the world. In Chapter 3 *Homo erectus* is discussed as a species. After describing the characteristics of this taxon from a palaeobiological, archaeological and behavioural perspective, the emphasis in the second part of this chapter is mainly placed on the palaeoecology of this taxon. In addition to reviewing the palaeoenvironmental data available for the principal sites, an account is given of our current knowledge of *Homo erectus* palaeoecology and how it is thought to relate to current theories about hominin dispersal.

Chapter 4 reviews ecomorphology conceptually as a scientific method. Here it is discussed how this method can be used on mammalian fossils and what its relevance is as a proxy for hominin palaeoecology. After giving an overview of the potential problems and limitations of the ecomorphological method, a review is given of the Cervidae family. This review includes a description of the taxonomy, ecology and evolution of the extant deer as well as a discussion of the fossil cervids that are found in Java and the surrounding region. A final section examines how ecomorphology can be applied to cervids.

Chapter 5 is made up of several sections pertaining to the methodology, materials and contributions of this dissertation. A first section discusses what research questions are addressed in this dissertation and how a number of hypotheses about *Homo erectus* palaeoecology and bahaviour will be tested. Later, a functional framework is outlined that provides a foundation on which the ecomorphological models can based. This section

concludes with a number of functional hypotheses that are later tested in the morphometric analyses. The chapter continues with a general discussion about GMM as a methodological approach and a more specific treatise of how it can -and will be- applied to (cervid) postcranial elements. The details of the morphometric protocols used in this dissertation are described, followed by a section that discusses the statistical analyses that are conducted on the morphometric data. Error testing methods are then outlined and the habitat groups that are used in the ecomorphological models are presented and justified. A final section discusses the extant and fossil materials that were used.

Chapter 6 reports on the results of the extant and fossil specimen analyses. The first half of the chapter deals with the results of the analyses of the extant species. Within this extant species section, I report the results of the calcaneus and the intermediate phalanx in the same way: after looking at the results of error testing and a test of the effects of sexual dimorphism, the main results of the ecomorphological analyses are provided. The second half of Chapter 6 deals with the results of the fossil analyses. This part of the chapter is divided in three sections: one section that discusses the results for Trinil and its most common species *Axis lydekkeri*, a second section that deals with the results for Kedung Brubus and *Cervus kendengensis*, and a third that gives the results for Sangiran.

Chapter 7 discusses the implications of the results for extant and fossil cervid ecomorphology, followed by a section that provides an interpretation of the habitats that were present in the vicinity of the sites during deposition. The chapter continues with a section that places the palaeoenvironmental reconstructions for the sites within the broader context of *Homo erectus* palaeoecology in Java and other parts of its range, and explores the implications for early hominin dispersal. After providing some further considerations about the used statistical tests, Chapter 8 gives an overarching conclusion with suggestions for future research.

2. Background

2.1 Introduction

As this thesis deals with the conditions that were present in Java during the Pleistocene it is imperative to first provide a summary of the conditions that are currently present there and that have shaped the island and the surrounding region in its present state. In section 2.2 a review is provided of the geological, climatological, vegetational and zoological setting of this region. In section 2.3 I present a *status quaestionis* of our current knowledge of the fossil record and discuss the biostratigraphy of Java.

2.2 The environmental context of Java

The island of Java is part of the Indomalayan archipelago which stretches between the Indian Ocean in the west and the Pacific in the east. With almost 25,000 islands, it is the largest archipelago on earth, covering more than two million km^2 (Moores & Fairbridge 1997). Indonesia, which takes up the largest part of the archipelago, is composed of a number of smaller island groups (Tomasick *et al*. 1997). Most important for this dissertation is the Greater Sunda Island chain, formed by Java, Sumatra, Borneo and Sulawesi (Simpson 1977, Aarsse 1993, Harrison *et al*. 2006). To the southeast of the Greater Sunda Islands lie the Lesser Sunda Islands, forming a second important chain to the east of Java, comprised of a number of smaller islands such as Bali, Lombok and Flores. In the northeast the Greater Sunda's are bordered by the Philippines, while in the south and in west they are surrounded by the Indian Ocean (Simpson 1977, Harrison *et al*. 2006) (Fig. 2.1). Java, being the southernmost island of the Greater Sundas, is approximately 127,000 km^2 in size. It has an elongated shape and measures about 1000 km from east to west and 180 km from north to south (Sevin 1993).

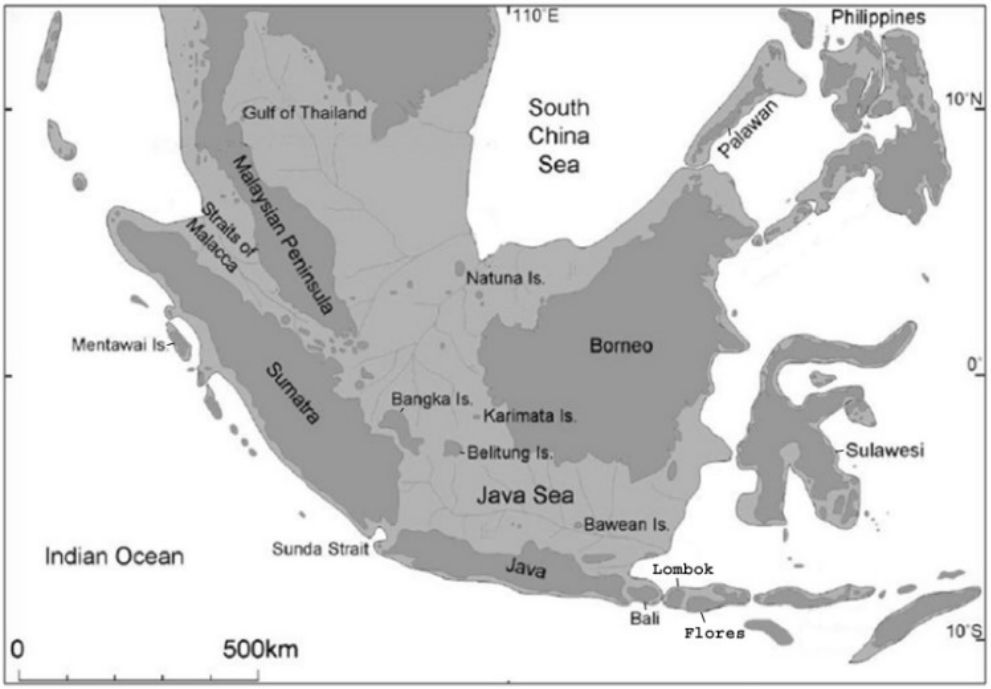


Figure 2.1: Map of sundaland during the last glacial maximum (adapted from Bird et al. 2005)

The present shape and topography of Java are largely the result of Indonesia's position at the intersection of four tectonic plates: the Eurasian plate, the Pacific plate, the Indo-Australian plate and the Philippine plate. Due to the subduction of the Indo-Australian plate under the Eurasian plate, the southern ridge of the latter is forced upward creating a number of Islands of which Java is part (Katili 1975, Bouteaux 2005). Borneo and Sumatra are thought to have been formed during the Early Tertiary (Zaim 2010). Of Java, only a small part in the west was emerged during this period. It was not until the Oligocene, in a context of increased tectonic activity, that the island developed its current shape (Hall 1998, Zaim 2010). After this, Java was subject to two other orogenic events that were instrumental in its formation: one during the Miocene and a final one during the Pleistocene (Saint-Marc *et al*. 1977, Zaim 2010).

Java lies on the southernmost border of the Sunda shelf, a pre-tertiairy platform that forms an extension of the Eurasian plate that is today for a large part covered by the Java Sea (Saint-

Marc *et al*. 1977). This shelf with its islands and shallow seas -that was at times in its geological past exposed above sealevel- is also called Sundaland (Harrison *et al*. 2006). To the east of Sundaland lies the Sahul shelf which is also partially covered by shallow seas and includes New Guinea and Australia. Although the Sunda- and Sahul shelfs are geographically close, they are separated from each other by deep marine trenches (Zaim 2010). Although this dissertation is focused on Java, geological and environmental changes that occurred on this island should be considered as part of larger events that took place in the whole Sunda region.

From the end of the Pliocene, when Sundaland became subject to intense tectonic activity (Zaim 2010), Java was also heavily influenced by glacio-eustatic sea level fluctuations (van den Bergh *et al*. 2001). During glacial episodes resulting in lower sea levels, large parts of the Sunda shelf were exposed, connecting the major islands, Borneo, Sumatra and Java, to the mainland (Voris 2000, Bird *et al*. 2005) (Fig. 2.1). While during the Early Pleistocene sea levels were still relatively stable and at about -70 meters below current levels, from 0.8 Ma, glacial-interglacial cycles intensified and increasingly oscillating sea levels are observed (Prentice & Denton 1988) (Fig. 2.2).

Today Java can be divided in a Western, Eastern and Central part (Whitten 1996). Regional topographical, climatic and vegetational differences between these parts are substantial. While West- and Central Java are generally rather mountainous, East Java is characterized by lowlands (Hertler 2004). In addition, in each of these three regions (East, Central and West) a number of physiographic zones can be found along a north-south altitudinal gradient. Van Bemellen (1949) divides the island in a number of physiographic units (Fig. 2.3):

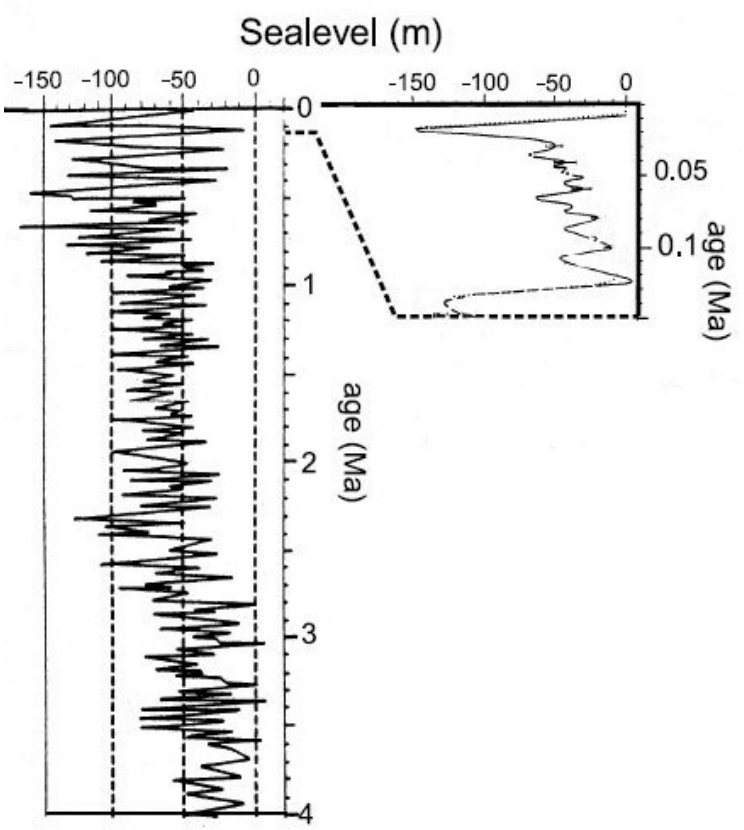


Figure 2.2: Sea level variations in over the last 4 Ma, based on $\delta^{18}O$ isotopic signatures of marine foraminifera (adapted from Prentice & Denton 1988 and van den Bergh et al. 2001). Note increasing sea level oscillations from the Middle Pleistocene.

A narrow strip of alluvial plains derived from river sediments is found along the northern coast. These are followed by a landscape of undulating to rolling hills, called the Northern Foothills, composed of sedimentary rocks of volcanic and marine origin. In the center of the island a cluster of young volcanic mountains is found that stretches more or less over the whole length of Java. Interspersed by these volcanic mountains there is also the Central Depression in the middle of the island, made up of Plio-Pleistocene alluvial and volcanic deposits (van Bemellen 1949, Whitten 1996). The south of the island is characterized by the Southern Mountains. These formations are composed of clastic deposits of Miocene age

mixed with marine sediments such as limestone (van Bemellen 1949, Whitten 1996, Bouteaux 2005).

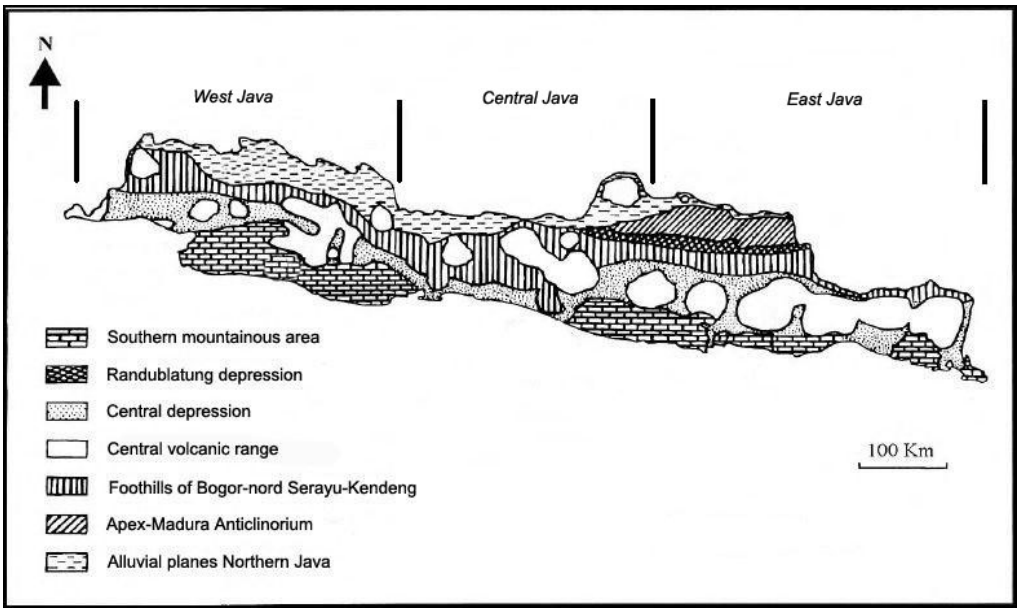


Figure 2.3: Physiographic zones of Java (adapted from van Bemmellen 1949).

Java currently has a marine tropical climate with temperatures that are almost constant throughout the year, but with substantial seasonal differences in rainfall (Yamada 2016). Climatic variations in Java are driven by differences in air masses within the Intertropical Convergence Zone (ITCZ). As a result of converging airstreams from the northern- and southern hemispheres, air uplifting and cloud formation lead to an increased rainfall pattern on the island (Whitten 1996, Aldarian *et al*. 2008). This generally humid regime is disturbed in the middle of the year by dry monsoon winds that mainly influence Central- and East Java (Whitten 1996). Due to alternating wet and dry seasons, rainfall is the most important seasonal ecological variable in Java (Amien *et al.* 1996, Whitten 1996). This picture is, however, complicated by local topography, as prominent mountains can create a rainshadow on leeward slopes, while exposing windward slopes to increased precipitation (Whitten 1996, Aldrian & Djamil 2008). As a result certain parts of West Java have an annual rainfall of as

much as 4000 mm, while some areas in East Java receive less than 1000 mm of rain per year (Yamada 2016).

Java is part of the diverse phytogeographical region Malesia, which includes a large area between peninsular Malaysia in the northwest and New Guinea in the southeast (Nooteboom 1992). This high biodiversity is explained by its geographical position in between different floristic regions (Mainland Southeast Asia, Australia), by the presence of mountains resulting in increased speciation at different altitudes and as a result of glacial-interglacial cycles periodically connecting and disconnecting the islands to the mainland (Whitten 1996, Cranbrook 2010). Although Java is among the less biodiverse islands in the Malesian region, it is still recognized by a wide range of vegetation types (Whitten 1996). As temperatures are constantly high and rainfall is governed by the monsoon regime, the climax vegetation on the island ranges from closed tropical rainforest to savannah (Sémah & Sémah 2012, Yamada 2016). The regional vegetation is also characterized by altitudinal gradients and includes lowland rainforest, lower and higher montane forest and subalpine vegetation (Backer & Bakhuizen van den Brinck 1965).

As the eastern part of Java has a longer and more severe dry period, its climax vegetation is drier than that of Western Java. The east is therefore mainly characterized by monsoon forest with taxa such as Mimosaceae and Poaceae being dominant (Sémah 1993, Bouteaux 2005, Yamada 2016). Some savannah with isolated *Acacia* trees is present in the far eastern Baluran area (Whitten 1996, Sémah & Sémah 2012). In the western part of the island, tropical moist deciduous forest can be found in the lowlands and some remnants of dipterocarp tropical lowland rainforest in the westernmost parts (Nooteboom 1992).

Zoogeographically Java is in the oriental realm, extending across most of Southeast Asia and the Indian subcontinent; and more specifically in the Sundaic subregion. The Sundaic

subregion encompasses the partially submerged Sunda shelf and is geographically delimited by a number of physical barriers restricting animal dispersal. In the northwest it is delimited by the Isthmus of Kra on the Thai peninsula (Hughes 2003) and in the south and the west by the Indian Ocean (Simpson 1977). The eastern boundary of the Sundaic subregion has for long been a matter of controversy and many lines have been drawn in the region in an attempt to delineate this zoogeographic area. Most of these lines cannot be considered absolute boundaries, as the distribution of taxa varies substantially between groups of organisms. For the distribution of mammals however, the so called Wallace's Line as modified by Huxley is the most relevant eastern boundary (Huxley 1868, Simpson 1977, Voris 2000, Harrisson 2006) (Fig. 2.4). The region East of Wallace's line is known as Wallacea, a transitional area between the Oriental realm and Australasian realm (Dickerson *et al*. 1928, Simpson 1977, van den Bergh 2001). Lydekker's line marks the eastern boundary between Wallacea and the Australasian realm (Simpson 1977, van den Bergh 2001).

Even though Wallace (1869) hypothesized that the effects of ancient sea level changes must have had an influence on the extant faunal composition of the Malay archipelago, it is now recognized that the current distribution of Southeast Asian mammals is largely a function of the geological and climatic events that took place over the course of the Tertiary and Quaternary (Hughes 2003, Vallejo 2011). When during glacial periods the larger islands of Sundaland (Java, Sumatra and Borneo) were connected to mainland Southeast Asia, terrestrial species were allowed to migrate between these regions. When, on the other hand, the islands were cut off from the mainland during interglacial periods, isolation of animal populations led to periods of increased endemism (Voris 2000, Bird *et al*. 2005, Cranbrook 2010).

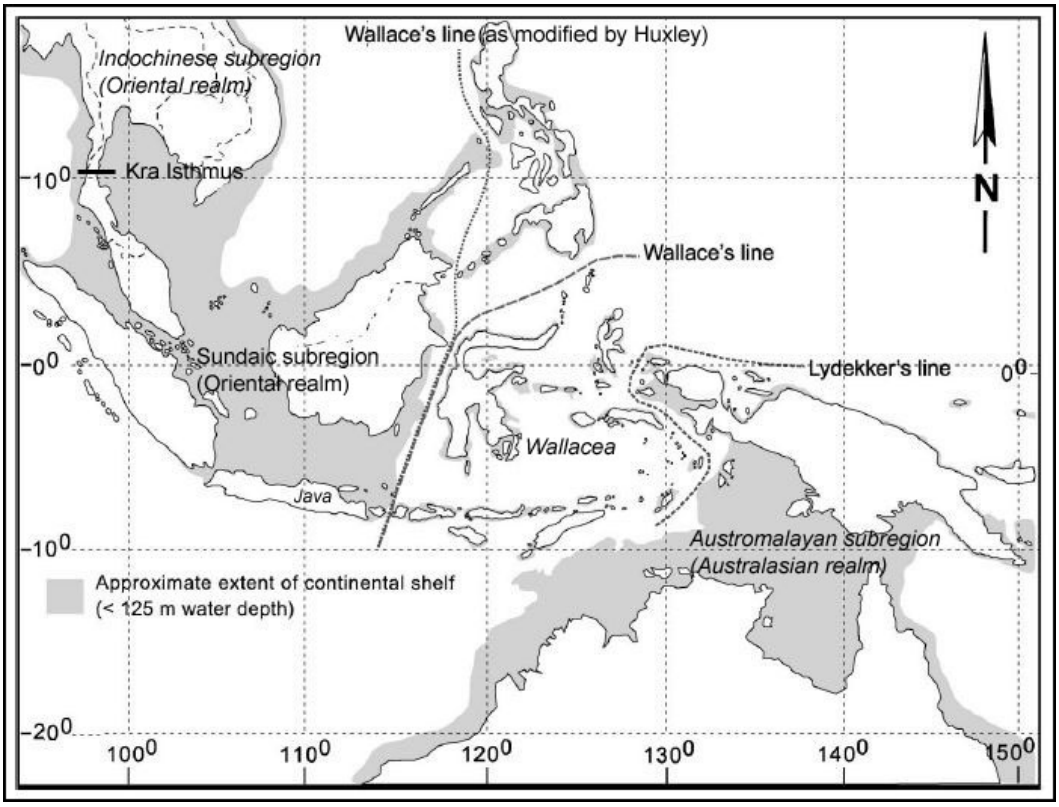


Figure 2.4: The Indomalayan region with main zoogeographic regions and boundaries (adapted from van den Bergh et al. 2001). In the west the Sundaic subregion is found, that forms the focus of this dissertation. Further to the east, and demarcated by Wallace's Line, the transitional region Wallacea is found. East of Wallacea, demarcated by Lydekker's line, the Austromalayan subregion is found.

As a result the fauna of Sundaland is much more similar to that of continental Southeast Asia than to the fauna of Wallacea with its impoverished mammal diversity and its high degree of endemism as a result of prolonged isolation (Bouteaux 2005). Java, as part of the Sundaic zoogeographical subregion, thus has the characteristics of a continental fauna, similar to that of Borneo, Sumatra, Southern Thailand and the Malay Peninsula. Its animal diversity is rich, both in number of species and in genera, although not to the same extent as Borneo and Sumatra (Corbett & Hill 1992, de Jong 1992). The relatively lower diversity in Java is the result of a number of factors. A first reason is that high biodiversity in Southeast Asia is usually concentrated in tropical rainforests, a type of vegetation only present in small

proportions in Java. A second reason is that the island of Java is relatively small and has long been the subject of intense volcanic activity. This must have increased the chances of local extinction for certain taxa (de Jong 1992). A third explanation is that the island has a long history of human disturbance of its ecosystems. It is likely that Java had a higher biodiversity during prehistoric times (Durand 1994, Whitten 1996).

Of the Greater Sunda Islands, Sumatra is most similar to Java in terms of mammalian composition. The two islands have approximately 43% of their mammal species in common, suggesting there was a connection between these landmasses for much of their geological past (de Jong 1992). Typical faunal elements associated with the Sundaic subregion are rhinoceroses (Rhinocerotidae), deer (Cervidae), tiger (*Panthera tigris*), pangolins (Manidae), treeshrews (Scandentia) and apes (Hominoidea) (de Jong 1992). These taxa are also present on Java, in addition to a number of endemics such as the Javan lutung (*Semnopithecus auratus*) or the Javan ferret badger (*Melogale orientalis*) (Whitten 1996). The majority of Java's mammal biodiversity is, however, composed of different species of rodents (Rodentia) and bats (Chiroptera) (Corbet & Hill 1992).

2.3 Quaternary palaeontology of Java and Sundaland

Our present understanding of the fossil record of the Sundaic subregion is limited, which is in part due to its unevenly distributed nature. Some parts such as Peninsular Malaysia (e.g. Tshen 2013, Ibrahim *et al*. 2012) or Sumatra (e.g. de vos 1983) are only known from a handful localities, while others such as Java are rich in fossil deposits and have a long history of palaeontological research (e.g. Dubois 1907, 1908, von Koenigswald 1933, 1934, 1935). Nevertheless, even for the Javan record many gaps remain to be filled (van den Bergh *et al*. 2001). Although it is likely that new discoveries and further research on existing collections

will resolve some of these problems (Louys 2007), I will for now restrict myself to Java to outline the evolution of the faunal record and biostratigraphy of the region.

Some controversy surrounds the appearance of the first mammals in Java. Van den Bergh and colleagues (2001) put it during the Early Pleistocene, about 1.5 to 2 million years ago, but some more recent research in West Java found bovid remains that are tentatively placed in the Late-Miocene to Early-Pliocene, at approximately 5 million years ago (Meijaard 2003a, Weinand 2005). Although this early date is not universally accepted (Meijaard 2003a), it is worth mentioning that von Koenigswald (in van Bemmelen 1970) also considered the first mammals in the region to be of Pliocene age. This was based on similarities between the material from Ci Julang (West-Java) and the fauna of the Tatrot beds which are part of the upper Siwaliks on the Indian subcontinent (von Koenigswald 1934, de Vos 1984, Bouteaux 2003). This would place the Ci Julang fauna between 2.5 and 3.4 Ma, taking more recent reevaluations of the Siwalik biostratigraphy into account (Barry *et al*. 1982). Pliocene alternating marine strata at Ci Julang may indicate an age of perhaps 2.7 million years (Shutler & Branches 1985). The stratigraphy and age of the fossils from this site remains, however, unresolved (Hooijer 1964, Meijaard 2003a). The earliest appearance of mammals on the nearby island of Sumatra is also unknown, but was much earlier, as some rare traces of terrestrial vertebrates (albeit birds) from the Oligocene suggest (Zonneveld *et al.* 2012).

As for the Pleistocene of Java, von Koenigswald (1934) was the first to propose a biostratigraphic scheme. Based on a several sites and by comparison with the faunas from continental Asia, von Koenigswald recognized six biostratigraphic units in Java, ranging from the Middle-Pliocene to the Holocene. An overview of the sequences defined by von Koenigswald (1934) is given in Figure 2.5. This classic scheme was however based on composite faunal assemblages and contained inconsistencies (de Vos & Sondaar 1982, de Vos

1985, de Vos 1996, van den Bergh *et al.* 2001). Consequently, a revised scheme was developed by de Vos and Sondaar (de Vos & Sondaar 1982, de Vos *et al.* 1982, 1994, de Vos 1985, Sondaar 1984) which is now generally accepted and also followed here (Fig. 2.6).

As opposed to von Koenigswald's (1934) original scheme, this biostratigraphy (de Vos & Sondaar 1982, de Vos 1985) was based only on fauna from single localities and fossils from sites with clear stratigraphic sequences (van den Bergh *et al*. 2001). The Ci Julang fauna, presented by von Koenigswald (1934) as the earliest stage in Java is not recognized as a discernable biostratigraphic unit in the new scheme. The oldest faunal stages proposed by de Vos and Sondaar are based on von Koenigswald's (1934) Kali Glagah biostratigraphic unit. De Vos and Sondaar, however, consider Kali Glagah as heterogenous and discern two different faunal stages in this unit: the Satir fauna and the Ci Saat fauna (de Vos & Sondaar 1982, de Vos *et al.* 1982, 1994, de Vos 1985, Sondaar 1984).

Faunal stages	**Age**
Sampung fauna:	Holocene
Ngandong fauna:	Late Pleistocene
Trinil fauna:	Middle Pleistocene
Djetis fauna:	Early Pleistocene
Kalih Glagah fauna:	Late Pliocene*
Ci Julang fauna:	Middle Pliocene

*Figure 2.5: Biostratigraphic scheme by von Koenigswald (1934) from young to old. *: In the new definition by the International Union for Geological Sciences, the lower boundry of the Pleistocene epoch is lowered from 1.806 Ma to 2.58 Ma (Gibbard & Head 2009). The Kalih Glagah fauna should in the context of this definition most likely be considered Early Pleistocene.*

The Satir faunal stage ranges between 2 and 1.5 million years and is usually considered an unbalanced island fauna (Sondaar 1984, de Vos *et al*. 1994, van den Bergh *et al*. 2001). Characteristic elements that are part of this fauna are an elephantoid (*Sinomastodon bumiajuensis*), a hippopotamus (*Hexaprotodon simplex*), cervids and giant tortoises (*Geochelone* sp.), mostly good swimmers with the ability of cross-sea dispersal (Meijaard 2003a). Nevertheless, little evidence is available for this period and certain researchers (Heaney 1985, Meijaard 2003a) have pointed out that the faunal composition of Satir may be subject to taphonomic or collection bias.

The seemingly isolated island conditions seem to continue in the Ci Saat fauna, that covers the time range between approximately 1.2 and 1 million years ago (de Vos & Sondaar 1982, de Vos *et al*. 1994, van den Bergh *et al*. 2001). Typical elements of this fauna are new forms of elephantoids (*Stegodon trigonocaphalus*) and hippopotamids (*Hexaprotodon sivalensis*), cervids (*Axis lydekkeri*, *Muntiacus* sp.), bovids and possibly a large cat (*Panthera* sp.) (de Vos *et al*. 1994, van den Bergh *et al.* 2001). The giant tortoises prelevant during the Satir faunal stage, disappear in this period (de Vos *et al*. 1994).

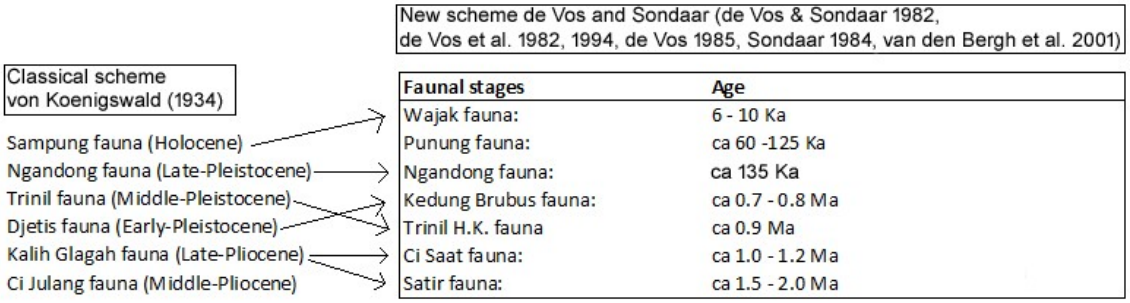


Figure 2.6: Biostratigraphic scheme by de Vos and Sondaar (de Vos & Sondaar 1982, de Vos et al. 1982, 1994, de Vos 1985, Sondaar 1984) and comparison with biostratigraphic scheme by von Koenigswald (1934).

An important implication of the new scheme by de Vos and Sondaar (de Vos & Sondaar 1982, de Vos *et al.* 1982, 1994, de Vos 1985, Sondaar 1984) is that a different place is given

to the assemblages of Trinil and Kedung Brubus in the chronology of Java. Instead of placing all material from Trinil together in one biostratigraphic unit, as von Koenigswald (1934) did, they only consider the main fossiliferous layer, also called the "Trinil Haupt-Knochen Schicht" or "Trinil H.K.", as contemporaneous (de Vos & Sondaar 1982, de Vos 1985). An important result of this different approach is that the biostratigraphic unit based on Trinil H.K. has a different place in the Javan biostratigraphy than the Trinil stage that von Koenigswald (1934) defined. While in the scheme of von Koenigswald (1934) the fauna of Trinil and Kedung Brubus were thought to be similar in composition, in the scheme of de Vos and Sondaar (de Vos & Sondaar 1982, de Vos 1985) the fauna of Kedung Brubus is substantially richer than that of Trinil H.K. De Vos and Sondaar (1982) explain this by considering Trinil H.K. as a fauna that is still more isolated from the mainland like the older Ci Saat fauna, whereas Kedung Brubus is characterized by a new mammal fauna that was able to migrate from the Asian mainland. As such the Trinil H.K. fauna is considered older in this scheme than the Kedung Brubus fauna. The Djetis fauna proposed by von Koenigswald (1935) is thought to be part of the Kedung Brubus fauna, as its faunal composition is remarkably similar to that of Kedung Brubus (de Vos & Sondaar 1982, de Vos *et al*. 1982, 1994). Although an older age for the Trinil H.K. fauna is suggested by Larick et al. (2001), in the model of de Vos and Sondaar, the age of Trinil H.K. is thought to be around 0.9 Ma (van den Bergh *et al.* 2001).

The age and presumed isolated nature of the Trinil H.K. fauna is not universally accepted. The hypothesis that Java was still more isolated during the Trinil H.K. stage is partially based on the presence of certain endemic species such as the proboscid *Stegodon trigonocephalus* and the bovid *Duboisia santeng* (de Vos & Sondaar 1982, de Vos *et al*. 1982, 1994). Meijaard (2003a) does not accept this and points out that *Duboisia santeng* was also described by Hooijer (1962) from deposits in Malaysia. For Heaney (1985) the large numbers of ungulates

and carnivores in the Trinil H.K. fauna are atypical for island ecosystems. Other problematic species in the Trinil H.K. fauna are orangutan (*Pongo* sp.) and gibbon (*Symphalangus syndactylus*?), both poor swimmers that are unlikely to have reached Java over sea (Meijaard 2003a). While the Malaysian collection with *Duboisia* cannot be restudied as it is unfortunately lost (Tshen 2013), it has by now been convincingly argued by Smith and colleagues (2009) that the supposed orangutan teeth from Trinil are in fact remains of *Homo erectus*. A recently reanalyzed femur nevertheless, most likely belonged to a gibbon (Hylobatidae) (Ingicco *et al.* 2014). Although the presence of certain elements in support of a more intensive exchange with the mainland should be aknowledged, I still follow de Vos and Sondaar (de Vos & Sondaar 1982, de Vos *et al.* 1982, 1994, de Vos 1985, Sondaar 1984) in this dissertation. When considering the assemblages of Kedung Brubus and Trinil H.K. as a whole, the former is still characterized by a richer and more continental character and therefore in support of de Vos and Sondaar's older age for Trinil.

Besides the taxa already mentioned, the Trinil H.K. fauna includes a relatively diverse range of mammal species including a number of carnivores (e.g. *Panthera tigris, Prionailurus bengalensis*), several bovids (e.g. *Bibos palaeosondaicus, Bubalus palaeokerabau*), cervids (e.g. *Axis lydekkeri*), suids (*Sus brachignathus*), primates (*Presbitis* sp., *Macaca fascicularis*) and a rhinoceros (*Rhinoceros sondaicus*) (van den Bergh et al. 2001). In addition, a number of mollusks, birds, reptiles and fish are known from this faunal unit (Storm 2012).

The Kedung Brubus fauna, as said, is characterized by more intensive mammal exchange with mainland Southeast Asia and may have coincided with a glacial phase (Musser 1982). In addition to the typical species already present during the Trinil H.K. phase, a number of new arrivals appear in the fossil record such as the bovid *Epileptobos groeneveldtii*, the one-horned rhinoceros (*Rhinoceros unicornis*), a hyena (*Hyena brevirostris*) and the Malayan tapir

(*Tapirus indicus*). The age of the Kedung Brubus fauna is estimated between 0.7 and 0.8 Ma (van den Bergh *et al.* 2001).

A large gap between the Kedung Brubus fauna and the Ngandong fauna exists in the fossil record of Java, of which little is known. According to Batchelor (1979) this period saw the extinction of many of the savannah-adapted species due to geographical isolation and the development of closed forest habitats. Despite the disappearance of a number of species, the fauna of Ngandong is considered similar to that of Kedung Brubus. This faunal stage is not well known, but includes several bovids (*Bibos palaeosondaicus, Bubalus palaeokerabau*), suids (*Sus macrognathus, Sus brachignathus*), cervids (*Cervus* (*Rusa*) sp.) and a primate (*Macaca fascicularis*) (van den Bergh *et al.* 2001). Based on biostratigraphic arguments, the age of the Ngandong fauna was originally estimated at approximately 135 Ka by van den Bergh et al. (2001). More recent radiometric dating of the *Homo erectus* bone bed has indicated an age between 108 and 117 Ka (Rizal *et al.* 2020).

Another new faunal unit proposed by de Vos and Sondaar (de Vos & Sondaar 1982, de Vos *et al.* 1982, 1994, de Vos 1985, Sondaar 1984) is the Punung fauna. This biostratigraphic unit is characterized by major changes in the fossil record. Many of the species present in the Kedung Brubus fauna have disappeared in the Punung fauna, but on the other hand a number of new species have arrived as well (van den Bergh *et al*. 2001). Typical for this period is a tropical rainforest fauna with large numbers of primates, including the earliest uncontested orangutan (*Pongo* sp.) specimens on Java (van den Bergh *et al*. 2001). Other new forms include Sumatran serow (*Capricornis sumatraensis*), Asian elephant (*Elephas maximus*), bearded pig (*Sus barbatus*) and banded pig (*Sus scrofa vittatus*) (van den Bergh *et al*. 2001). Most of these new immigrants probably arrived before 70 Ka, at a time when sea levels were 40 to 65 meters lower than today, but after the glacial maximum at 135 Ka (van den Bergh et al. 2001). Van den Bergh and colleagues place it between 125 and 60 Ka, with a possible age

of 80 Ka (van den Bergh et al. 2001). Westeway *et al*. (2007) give a somewhat older age of 128 to 118 Ka, based on absolute dates obtained from luminescence and uranium series.

The youngest stage in the biostratigraphic scheme is the Wajak fauna. Although it is considered to be of Holocene age in this classic scheme (de Vos & Sondaar 1982, de Vos *et al.* 1982, 1994, de Vos 1985, Sondaar 1984), more recent radiometric dates suggest a minimum age of at least 37.4 to 28.5 thousand years old (Storm *et al*. 2013). The faunal record is impoverished compared to the Punung fauna. A number of forest-adapted species, such as orangutan (*Pongo* sp.) and tapir (*Tapirus indicus*) disappeared from the record as they were apparently unable to cope with the dryer conditions prevalent during this period. Most of these lost species were not replaced by new ones (van den Bergh *et al*. 2001).

3. *Homo erectus*: significance, dispersal and palaeoecology

3.1 Introduction

Homo erectus was a large brained, relatively small toothed hominin (Anton & Swisher 2004) that ranged in age from 1.8 or 1.9 million years ago in East Africa (Larsen *et al*. 1998, Anton 2003, Anton *et al.* 2016) to 250-400,000 years ago (Larsen et al. 1998, Anton *et al.* 2016), or even 100,000 years ago or less in Indonesia (Swisher *et al*. 1996). It was the first hominin to venture out of Africa into other areas of the Old World (Anton & Swisher 2004). Its fossils are found in South Africa, East Africa, North Africa, in the Middle East and in South, Southeast and East Asia. Possibly it was present in Europe (Dunsworth &Walker 2002, Anton 2003). This chapter first gives an overview of the known fossil record for this species and its taxonomic position, followed by an account of the characteristics that made it unique. After providing a review of palaeoecological reconstructions of *Homo erectus* sites, the possible causes and underlying processes that were at the basis of its dispersal are discussed.

3.2 Fossil record

Although the late 19th century had already seen the discovery of the Neanderthal (*Homo neanderthalensis*) in Europe, the fossil femur, skullcap and molar that Dubois found at Trinil in the 1890's were the first remains of a more archaic human ever to be discovered (Rightmire 1990). While some (Shipman & Storm 2002) consider this event the beginning of palaeoanthropology as a scientific discipline, what is certain, is that Dubois' discoveries were significant in that they represented the first finds and type-specimens of *Homo erectus* (Leakey & Slikkeveer 1993). Despite initial skepticism about the taxonomic position of the Trinil fossils, other, similar finds would soon be discovered in Africa and Asia (Fig. 3.1) that would ultimately lead to the recognition Dubois' findings and the acceptance of *Homo erectus* as a species (Dunsworth & Walker 2002).

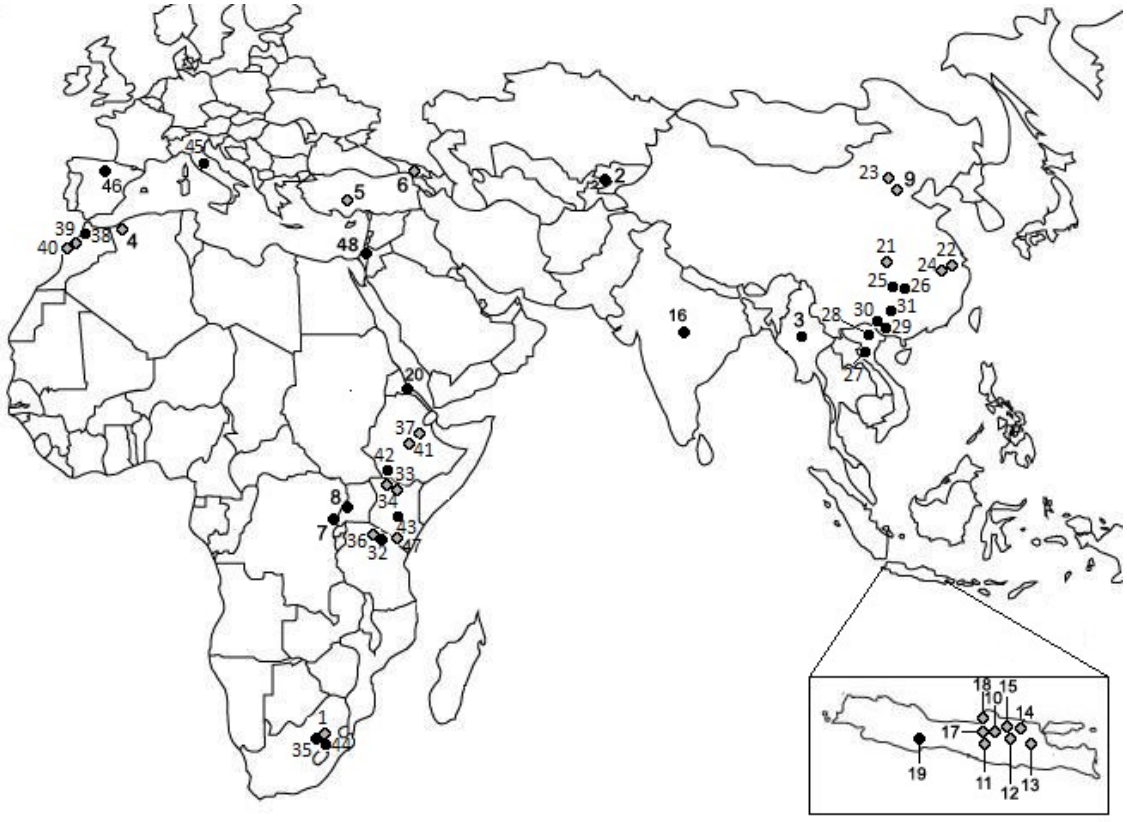


Figure 3.1: Map with possible- (black dots) and probable/definite (grey dots) localities with Homo erectus fossils. With the exception of Ceprano and Atapuerca, other possible localities in Europe have been excluded due to the unclear taxonomic status of early Homo on this continent (see e.g. Mounier 2009). 1. Swartkrans, 2. Sel'Ungur, 3. Nwe Gwe Hill, 4.Ternifine, 5. Kocabas, 6. Dmanisi, 7. Ishango, 8. Nyabusoni, 9. Zhoukoudian, 10. Trinil, 11. Sangiran, 12. Kedung Brubus, 13. Mojokerto, 14. Ngandong, 15. Ngawi, 16. Hathnora, 17. Sambungmakan, 18. Patiayam, 19. Cisanga, 20. Buia, 21. Lantian, 22. Tangshan, 23. Nihewan Basin, 24. Hexian, 25. Longgupo, 26. Jianshi, 27. Lang Trang, 28. Tham Khuyen, 29. Sanhe, 30. Mohui, 31. Liucheng, 32. Ndutu, 33. Koobi Fora, 34. Nariokotome, 35. Drimolen, 36. Olduvai, 37. Middle-Awash, 38. Sale, 39. Sidi Abderrahman, 40. Thomas Quarries, 41. Melka Kunture, 42. Omo, 43. Baringo, 44. Gladysvale, 45. Ceprano, 46. Atapuerca, 47. Olorgesailie, 48. Ubeidiya (see body of text for references).

In the 1920's, such new finds were made at Zhoukoudian, close to Beijing (Black 1927, Rightmire 1990). These cave deposits were rich in hominin remains that were classified as early humans and placed under the nomen *Sinanthropus pekinensis* (Black 1927). The age of these fossils remains controversial until today, but is likely early Middle Pleistocene (Zhou *et*

al. 2000), perhaps between 400 and 600 Ka (Zhu & Zhou 1994, Shen *et al*. 1996, Zhou *et al*. 2000, Dennell 2009). Due to the remarkable similarity between *Sinanthropus* and Dubois' *Pithecanthropus,* the finds would later be synonymized into *Homo erectus* (Weidenreich 1943, 1951, Santa Luca 1980).

Shortly after the Chinese discoveries, new finds were made in Java at Ngandong (Oppenoorth 1932, Barstra 1987), a site dated around 135 ka (van den Bergh *et al.* 2001). Although the taxonomic position of the Ngandong hominins is still controversial (Dubsworth & Walker 2002), this form is usually considered a late representative of *Homo erectus* (Santa Luca 1980). Meanwhile, a mandible from Kedung Brubus (0.7-0.8 Ma), previously found by Dubois but initially described as *Homo* sp. (Dubois 1891), was restudied and also placed under the hypodigm *Homo erectus* (Dubois 1924, McGregor 1925, Tobias 1966a).

A possibly much older specimen of *H. erectus* was found in 1936 by von Koenigswald near Perning (von Koenigswald 1940, Dunsworth & Walker 2002). Some controversy surrounds this specimen due to its purported age (Rightmire 1990), as the radiometric dates of the (supposedly) surrounding sediments have indicated an age of approximately 1.8 Ma (Swisher *et al*. 1994). As the original find location of the fossil is not known with certainty this age is not universally accepted (e.g. Morwood *et al*. 2003, Anton & Swisher 2004, Matsu'ura *et al*. 2020).

A more rich hominin site studied by von Koenigswald from the 1930's, was Sangiran (Hooijer 1964). With more than 60 individuals (mostly crania and mandibles) it is the richest palaeoanthropological site in Java (Sartono 1971, Simanjuntak 2001). The age of the Sangiran hominins is controversial. Based on radiometric dates, Larick and colleagues (2001) consider most of the *Homo erectus* finds around 1.1 to 1.3 million years old, but its earliest appearance in the Pucangan formation is already around 1.6 Ma. This would be in line with the early

dates proposed by Swisher et al. (1994). Others (Sémah *et al.* 2002, Matsu'ura et *al.* 2020) have, nevertheless, suggested a later appearance of *Homo erectus* -around 1.3 Ma- in the Sangiran record and on Java. The youngest *Homo erectus* finds from this site are perhaps dated at 700 Ka or less (Sémah *et al.* 2002).

The presence of more archaic, robust specimens (e.g. Sangiran 4, 6 and 31), found in the older layers and a more classic type of *Homo erectus* found in the younger layers (e.g. Sangiran 1 and 17) has led to some debate about how many distinct species were present at the site (Rightmire 1990, Simanjuntak 2001). This led Weidenreich and von Koenigswald to consider the earlier type as a separate taxon named *Meganthropus paleojavanicus* (Schwartz & Tattersall 2003). Both groups are now, however, by most palaeoanthropologists considered to be different forms of *Homo erectus* (Simanjuntak 2001, Schwarz & Tattersall 2003). The Ngandong fossils are considered a third, even more progressed, form of *Homo erectus* in this model (Simanjuntak 2001).

Even though the 1920's saw the discovery of *Australopithecus* in South Africa (Dart 1925) and *Homo rhodesiensis* (Woodward 1921) or perhaps *Homo heidelbergensis* (Balzeau *et al.* 2017) in Zambia, more archaic members of the genus *Homo* were not found in Africa during the first half of the 20th century. This changed after WWII when attention in palaeoanthropology shifted more towards this continent. In 1949 at Swartkrans, South Africa, new Early Pleistocene (Vogel 1985, Curnoe *et al.* 2001) fossils were found, that would be described as *Telanthropus capensis* (Broom & Robinson 1950). This species was later synonymized with *Homo erectus* (Mayr 1950, Dunsworth & Walker 2002). More recently some other, fragmentary remains of *Homo* sp. have been discovered in the Sterkfontein region (Gladysvale, Drimolen), but it is uncertain whether they can be classified as *Homo erectus* or another Pleistocene form (Moggi-Cecchi *et al.* 2010).

In the second half of the 20th century hominin finds were also being made in northern Africa. At Ternifine (Algeria) two 700.000 year old (Geraards *et al.* 1986) mandibles were discovered (Arambourg 1955), while another jawbone was found at the Middle Pleistocene site of Sidi Abderrahman in Morocco (Arambourg & Biberson 1956). Some years later more cranial- and mandibular remains were found in Morocco at the Middle Pleistocene sites of Salé (Jaeger 1975, 1981) and Thomas Quarries (around 400 Ka) (Sausse 1975, Hublin 1985). These new finds were quickly recognized as similar to the African and Asian *Homo erectus* fossils (Arambourg 1955), but were initially placed under their own nomen: *Atlanthropus mauritanicus*. Eventually the species was also subsumed under *Homo erectus* (Mayr 1950, 1963, Dunsworth & Walker 2002).

Since the 1950's East Africa has become prominent in palaeoanthropological research and many new fossils have come to light in this part of the continent. Of importance are a number of purported *Homo erectus* finds made at the Olduvai Gorge in northern Tanzania, including both cranial (e.g. OH9, OH12) and postcranial remains (Leakey 1959, 1966, 1971a, 1971b). At times these fossils were found in association with lithic artefacts, providing for the first time a clear link between *Homo erectus* and the Acheulian industry (Leakey 1971b, Dunsworth & Walker 2002). The *Homo erectus* remains recovered at Olduvai are thought to range in age between approximately 1.6 and 0.6 million years (Rightmire 1979). Ndutu, a site somewhat to the south of Olduvai, produced some remains of less clear taxonomic affinity. A skull fragment found there may belong to *Homo erectus* (Rightmire 1983).

Further to the North, in the area of Lake Turkana in Kenya, some of the most prolific finds of *Homo erectus* have been made. Many of the initially discovered hominin fossils were fragmentary and were cautiously identified as *Homo* sp. (Leakey 1973) but more complete finds were made later (Leakey 1974, Leakey & Walker 1976, Spoor *et al*. 2005, Boyle & Desilva 2015), that have been assigned to *Homo erectus* (Rightmire 1990). Amongst the

specimens from East Turkana, more specifically from Koobi Fora, are the oldest known *Homo erectus* specimens. Some of the fossils (e.g. KNM-ER 3228 and KNM-ER 3733) date to 1.8- or even 1.9 Ma (Leakey & Walker 1976, Day 1971).

The best preserved *Homo erectus* fossil from East Africa is nevertheless a specimen from the banks of the Nariokotome River (West Turkana). KNM-WT 15000 is a sub-complete skeleton of a young male, dubbed "Turkana boy" (Brown *et al*. 1985, Rightmire 1990). Although the fossil belongs to a sub-adult, its morphology is similar to that of the other Turkana specimens, confirming its classification as *H. erectus* (Rightmire 1990).

More to the south, two well preserved mandibles (KNM-BK 67 and KNM-BK 8518), some postcranial remains and a number of Acheulean stone tools were recovered at Lake Baringo (Leakey *et al*. 1969, van Noten 1983). The mandibles are morphologically distinct from the other *H. erectus* remains from East Africa and their classification therefore remains uncertain (Rightmire 1990). Furthermore, a partial skull identified as *Homo erectus* (KNM-OL 45500), was found in association with Acheulean stone tools at Olorgesailie (approximately 0.9 Ma) (Potts *et al.* 2004).

Close to the Turkana Basin, but on the the Ethiopian side of the lake, hominin remains were found at Omo. The age of these remains is unclear, but may be as young as 130 Ka (Day & Stringer 1982). Although some of the fossils found there are now considered *Homo sapiens*, some of them (e.g, Omo II) show a morphological similarity to *Homo erectus* (Day & Stringer 1982). Since the 1980's other Ethiopian finds have been assigned to *Homo erectus* as well, including a mandible (Garba IV) excavated at Melka Kunture (Zilberman *et al*. 2004), dated between 0.7 and 1.7 Ma (Raynal *et al.* 2004) and several fossil remains found at Bouri (1 Ma) and Bodo (Middle Pleistocene) in the Middle Awash valley (Asfaw 1983, Asfaw *et al.* 2002).

In addition to the finds from Kenya, Tanzania and Ethiopia, some scattered fossils are known from neighboring East African countries. The identification of these fossils remains uncertain. At Buia (Eritrea) a cranium and some pelvic fragments were found (Martinez-Navarro *et al*. 2004). The skull, dated between 0.6 and 1.4 Ma, was provisionally described as *erectus-like* (Martinez-Navarro *et al*. 2004). A recently restudied molar (ISH25) from Ishango, in the most western part of the Democratic Republic of Congo may belong to an early species within the genus *Homo* (Crevecoeur *et al*. 2014) and a fossil from Nyabusosi in Western Uganda was identified as *Homo* cf. *erectus* (Senut *et al.* 1987).

The important discoveries in Africa did not mean research in Asia came to a stop during the second half of the 20th century. At Sambungmacan, on Java, *Homo erectus* specimens were discovered in the 1970's, of which mainly cranium SM1 is of importance as it is the only specimen that clearly came from a stratified context (Delson *et al*. 2000, 2001). These remains were morphologically similar to the Ngandong specimens (Delson *et al.* 2001) and together with a number of fossils found at Ngawi in the 1980's (Sartono 1991, Kaifu *et al.* 2015), they may represent the youngest *Homo erectus* finds in Asia (Swisher *et al.* 1996). Their exact age, nevertheless, remains controversial (see e.g. Swisher *et al.* 1996, Indriati *et al.* 2011). Furthermore, some more isolated dental remains have been found at Patiayam (Zaim 1998) and possibly at Cisanga (Kramer *et al*. 2005).

The last decades of the 20th century saw a number of new discoveries in China as well. North of Zhoukoudian, at Xujiayao in the Nihewan Basin, a number of archaic human remains have been found (Wu & Poirier 1995, Ao *et al*. 2017). The classification of the fossils is uncertain, but they probably represent *Homo erectus*. With an approximate age of 260 to 370 Ka they are younger than the Zhoukoudian fossils (Ao *et al.* 2017). Further to the south, but still within the palaearctic realm, a few other finds have been assigned to *Homo erectus*. At Lantian, *Homo erectus* was identified at two localities: Chengjiawo and Gongwangling. At

the open air site of Gongwangling some poorly preserved cranial fragments can probably be assigned to *Homo erectus* (Wu & Poirier 1995). Their age is unclear, but has in the past been determined as either 750 to 800 Ka (An *et al*. 1990), 1.15 Ma (An & Ho 1989), or more recently, based on new palaeomagnetic dates, around 1.63 Ma (Zhu *et al*. 2015). This could make the fossils from this site, the oldest known Asian hominins above the Qinling mountain range and would place them in the age range of other early Asian finds such as those from Sangiran (Matsu'ura *et al.* 2020) and Dmanisi (Gabunia *et al.* 2002b, Ferring *et al.* 2011). An isolated mandible of *H. erectus* that was discovered at Chengjiawo (Zhu & Zhou 1994) was dated to 650 Ka (Liu 1985a). In addition, there are also a number of archaeological assemblages, such as those from Majuangou III (Zhu *et al.* 2004), Shangshazui (Ao *et al*. 2010), Donggutuo (Pei *et al.* 2009) and Xiaochangliang (Peterson *et al.* 2003) (all from the Nihewan Basin) and Shangchen (Lantian) (Zhu *et al*. 2018), which can be considered chronologically compatible with a *Homo erectus* assignment. The latter archaeological sites can be placed in the Early Pleistocene (see section 3.5.2.2) and for Shangchen even an age of 2.1 Ma has been proposed (Zhu *et al.* 2018).

Hexian, another more southern site, has provided better preserved cranial remains (Wu & Poirier 1995). The remains recovered there in the 1980's probably represent the youngest occurrence of *Homo erectus* in China and are dated between 150 and 190 Ka (Chen *et al*. 1987). Although the identification of these specimens as *Homo erectus* is generally accepted, the relationship between the fossils from Hexian and the other Asian finds is not well understood (Wu & Dong 1982, Dong 1989, Wu & Poirier 1995). A fragmented partial cranium found at the Middle Pleistocene site of Tangshan represents another find within the palaearctic region of China. This specimen showed some morphological differences from the Zhoukoudian fossils, but was nevertheless classified as *Homo erectus* (Liu *et al*. 2005).

As has been described, a number of sites have produced evidence for the presence of *Homo erectus* in China north of the Qinling Mountain range. Below this geographical barrier, the presence of this species is less certain on the mainland. This region was during the Early and Middle Pleistocene associated with the typical "*Stegodon-Ailuropoda* fauna" (Kahlke 1961). In the past *Homo erectus* has been reported at a number of *Stegodon-Ailuropoda* sites, but such classifications have more recently been questioned (Ciochon 2010). At Mohui Cave, in the Guangxi province, a substantial number of Early Pleistocene faunal remains were recovered, amongst which there were a number of teeth of giant ape (*Gigantopithecus*) as well as two teeth of a smaller hominoid (Wang *et al.* 2005). The teeth were initially placed under the nomen *Homo erectus*, but were later re-classified as "Hominoid indet." as the size of the molars exceeds that of the known *Homo erectus* teeth (Wang *et al*. 2007, Ciochon 2010). Moreover, the fossils show a morphological similarity to the Miocene ape *Lufengpithecus*, leading some (e.g. Ciochon 2009, 2010) to suspect the presence of an unidentified chimpanzee-sized ape in the Pleistocene of mainland Southeast Asia. As a result, doubt has been cast on most *Homo erectus* identifications in this region and the species may not have been present in any of the *Stegodon-Ailuropoda* assemblages.

This may for example be the case for Jianshi Cave in the Hubei province, where dental remains similar to the Mohui teeth were discovered (Gao 1975). Although these were initially identified as "australopithecid" (Gao 1975) and later as *Homo erectus* (Zhang 1984), the classification of these teeth remains unclear and they may belong an undescribed ape (Ciochon 2010). At Longupo Cave, in the Sichuan province, a mandible was discovered and dated between 1.8 and 2 Ma (Huang *et al.* 1991, 1995, Huang & Zheng 1999). It has been variously identified as an early representative of the genus *Homo* (Huang *et al.* 119, Ciochon 2010) or a relative of the orangutan (*Pongo*) (Schwartz & Tattersall 1996). Furthermore, at Sanhe Cave in the Guangxi province, some medium sized hominid teeth were excavated as

part of a *Stegodon-Ailuropoda* assemblage (Jin et al. 2009). The finds were in this case identified as "cf. Homininae" or "cf. Ponginae" (Ciochon 2010).

In Vietnam, the same problem presents itself. Here hominoid teeth are also found at times in the *Stegodon-Ailuropoda* fauna. At Lang Trang cave in the Ba Thuoc province, fieldwork was explicitely started with the purpose of documenting *Gigantopithecus blackii* and *Homo erectus* (Ciochon *et al*. 1990, Ciochon 2010). Although no *Gigantopithecus* fossils were found amongst the large numbers of excavated fauna, a few teeth were attributed to *Homo* sp. (Ciochon *et al*. 1990, Long *et al.* 1996). It is, however, likely that the human teeth are of a younger age than the *Stegodon-Ailuropoda* fauna found in this cave, suggesting the absence of *Homo* during the Early and Middle Pleistocene at this site (Ciochon 2010). Another cave in Vietnam that was often cited as containing *Homo erectus* together with *Gigantopithecus*, was Tham Khuyen in the Lang Son province (Ciochon 2010). This site contained large samples of animal remains, including supposedly contemporary dental remains of *Homo erectus* and *Gigantopithecus* (Kha & Long 1976, Ciochon *et al*. 1996). Later reanalysis of the teeth revealed that they more likely belong to orangutan (*Pongo* sp.) or a new ape taxon, named *Langsonia liquidens* (Schwartz *et al.*1995).

South- and Central Asia largely remain *terra incognita* as far as *Homo erectus* remains are concerned. Certain finds have been claimed to belong to *Homo erectus*, but most are controversial. In central Myanmar there is report of a 200,000 year old *Homo erectus* maxilla from Nwe-Gwe Hill in the Chindwin Basin (Ba Maw 1995). This identification is nevertheless unconfirmed and its association with Neolithic tools make an Early or Middle Pleistocene age unlikely. A somewhat more convincing find is known from Hathnora in India. A cranium, found alongside two clavicles and a rib fragment, are possibly the only known "pre-*sapiens*" specimens from the Indian subcontinent (Sonakia 1984, 1985, Sankhyan *et al.* 2012). The skull is probably of Middle Pleistocene age and has been variously identified as

Homo erectus (de Lumley & Sonakia 1985) and early *Homo sapiens* (Kennedy *et al.* 1991). Another claim comes from a cave site in the Alai mountain range in Kyrgystan. During the 1980's a Soviet team excavated an assemblage of animal bones there that included some human remains (Islamov *et al*. 1988). The site was dated around 126 Ka (Markova 1992) and according to the excavators, contained a juvenile humerus and some teeth of *Homo erectus* (Islamov *et al*. 1988). Others (Glantz *et al.* 2004) have argued that the humerus can only be identified as *Homo* sp. while the teeth probably belong to cave bear (*Ursus spelaeus*).

In Western Asia more is known about the species. In Turkey a skull fragment, identified as *Homo erectus* was found at Kocabas (Kappelman *et al*. 2008). This specimen, discovered in a travertine mine, is most likely of an Early to Middle Pleistocene age (Vialet *et al.* 2012) and perhaps older than 1.1 Ma (Lebatard *et al*. 2014). Some remains found at Ubeidiya (Israel) fall within the age range of *Homo erectus*, but do not allow taxonomic classification beyond the generic level (*Homo* sp.) (Tobias 1966b). The fossils, found alongside large amounts of lithic artefacts and animal bones (Tchernov 1988, Belmaker *et al.* 2002) are thought to be 1.4 million years old (Tchernov 1988).

Perhaps more important, are a large number of cranial and postcranial fossils that have been found at Dmanisi in Georgia. These well preserved specimens belonged to a hominin with clear morphological affinities to African and Asian *Homo erectus* (Lordkipanidze *et al.* 2013). The layers where the fossils were found are estimated to be approximately 1.7 million years old (Gabunia *et al.* 2000b) and most likely represent the oldest known *Homo erectus* finds outside of Africa (Lordkipanidze *et al.* 2013, Dunsworth & Walker 2002). Characteristic for the Dmanisi remains are their relatively small brains combined with postcranial body proportions closer to modern humans (Lordkipanidze *et al.* 2013).

Europe has a long tradition of palaeoanthropological research and a substantial number of Pleistocene hominins have been found there. Some of these finds are contemporary with the *Homo erectus* finds from Asia and Africa. In part influenced by the assumption that the occupation of Europe was a relatively late phenomenon (see Roebroeks 2001) and because a large number of the European fossils are too idiosyncratic to be included in *Homo erectus*, most archaic *Homo* specimens from this continent are classified as separate taxa (Eldredge & Tattersall 1982, Smith 2002). Forms that were presumably contemporary with *Homo erectus*, were *Homo heidelbergensis* (Soetenack 1908, Rightmire 1990, Mounier 2009) and *Homo antecessor* (Bermudez de Castro *et al*. 1997, Smith 2002). Although most researchers (Rightmire 2001, Stringer 2010) aknowledge the existence of a separate lineage in Europe, some rare specimens may nevertheless conform morphologically to the Asian or African *Homo erectus* finds, to the extent that they can be included in this species (Dunsworth & Walker 2002). This may be the case for a calvarium from Ceprano in Italy (Ascenzi *et al.* 1996, Rightmire 1998), that is according to more recent estimates ca. 350.000 years old (Normade *et al.* 2011). Other early fossils with a potential taxonomic affinity with *Homo erectus*, are those from Sierra de Atapuerca in northern Spain (Carbonell *et al*. 1995). Here, in several caves, hominin remains were found and identified as *Homo heidelbergensis* and/or *Homo antecessor* (Carbonell *et al.* 1995, 2008). Mainly some of the older specimens from Gran Dolina (Carbonell *et al*. 1995, Bruner *et al.* 2017) and Sima Del Elephante (Carbonell *et al.* 2008), (respectively dated at 0.8 and 1.2 Ma), are identified as *Homo antecessor* and may represent an intermediate form between *Homo erectus* and *Homo heidelbergensis*, evolved from African *Homo erectus* stock (Carretero *et al.* 1999, Bruner *et al.* 2017). Their taxonomic status nevertheless remains controversial and the specimens may in fact also be close to the North African *Homo mauritanicus,* now considered *Homo erectus* (see Mounier 2009, Stringer 2010) or a younger member of the genus *Homo* (Baab 2014).

3.3 Taxonomy, anatomy and evolution

The taxonomic position of *Homo erectus* should be considered within the wider systematic framework of the Genus *Homo* (Dunsworth & Walker 2002). The definition of our genus has changed considerably over the years as a result of new palaeontological finds and for now remains unclear (Collard & Wood 2015). By most accounts the *Homo* lineage emerged somewhere between 2 and 3 Ma in Africa from a still unknown ancestral species (Collard & Wood 2015, Kimbel & Vilmoare 2016). It is generally agreed that *Homo habilis*, probably the ancestor of all other members of *Homo,* evolved from a species of *Australopithecus* during this period (Dunsworth 2010). Found in eastern Africa from around 2.8 Ma (Villomoare *et al*. 2015), *Homo habilis* is thought to have given rise to *Homo erectus* somewhere around 1.8 or 1.9 Ma (Dunsworth & Walker 2002, Dunsworth 2010). There is nevertheless evidence of chronological and geographical overlap of the two species, as well as with a third member of the genus, *Homo rudolfensis* and the robust australopithecines (Dunsworth 2010). In addition, it is thought that *Homo erectus* itself may in turn have been ancestral to several other Pleistocene species such as *Homo heidelbergensis* (Mounier 2009), *Homo sapiens* (Smith 2002) and *Homo floresiensis* (Morwood *et al.* 2004).

Given its derived morphology *Homo erectus* is relatively easily differentiated from *Australopithecus* (Dunsworth 2010). The morphological differences from other members of the genus are more subtle and have led in the early 20th century to a high number of names (e.g. *Sinanthropus, Atlanthropus, Telanthropus*,…) being proposed for the different *Homo* fossils (Smith 2002). Many of these new taxa were raised without much consideration for taxonomic protocol (Smith 2002) and eventually resulted in the 1950's in a new paradigm that synonymized many of these forms into a simpler taxonomic scheme (Mayr 1950, 1960).

Consequently, most Early and Middle Pleistocene *Homo* species were lumped under *Homo erectus*, *Homo sapiens* and *Homo habilis* (Anton & Swisher 2004). In the last few decades growing dissatisfaction with this simplified model has led to the resurrection of some of the old taxa, as well as to the proposition of some new species (Eldredge & Tattersall 1982, Smith 2002). An important exponent of this new evolution was the idea that the often more gracile African *Homo erectus* specimens merit their own binomen (*Homo ergaster*), separate from the Asian fossils (*Homo erectus* sensu stricto) (Groves & Mazak 1975). According to some researchers (e.g. Wood 1994) it was the African *Homo ergaster* that led to *Homo sapiens*, while the Asian *Homo erectus* sensu stricto was separated from the direct lineage to modern humans (Dunsworth & Walker 2002). The validity of *Homo ergaster* is nevertheless questioned and others (e.g. Rightmire 1990, 2001, Baab 2008) have maintained a model where the African form is merely a regional variant of *Homo erectus* (sensu lato).

The addition of *Homo rudolfensis*, another closely related form, further complicates the family tree (Dunsworth & Walker 2002). The validity of this species, only known from a cranium from Koobi Fora and a mandible from Malawi is also the subject of intense debate (Dunsworth 2010). According to some (Wood & Collard 1999) it should be considered a sister taxon of *Homo erectus* and/or *Homo habilis*. Others (e.g. Baab 2008) think it should be subsumed into *Homo habilis*.

A third discovery with important implications for the taxonomic classification of *Homo erectus* is that of the Dmanisi hominins (Lordkipanidze *et al.* 2013). The Georgian specimens are especially important in that they show high intra-group morphological variation. As comparative morphometric analysis has demonstrated that this variation is not unlike that found in extant *Homo* and *Pan*, it suggests that some other *Homo* fossils, traditionally considered as separate species, fall within the morphological variation of *Homo erectus* (Lordkipanidze *et al.* 2013). This interpretation is on the other hand not universally accepted

(see e.g. Collard & Wood 2015) and it is likely that the debate will continue for the time to come. For this dissertation it will be sufficient to mention that I follow the conservative approach of Rightmire (1990) and consider the Asian (*Homo erectus* s.s.), African (*Homo ergaster*) and Georgian fossils as one species: *Homo erectus* (sensu lato).

Similar to Europe and Africa, Asia also saw the establishment of a number of new Pleistocene hominin taxa (e.g. *Meganthropus*, *Sinanthropus*, *Pithecanthropus*,…) during the 20th century. Most of these forms have later been subsumed into *Homo erectus* (Dunsworth & Walker 2002). Until recently few researchers still split the Asian lineage (except e.g. Sartono *et al*. 1995, Tyler 2001), but some tantalizing new finds of the last few years have rekindled the debate. One important discovery in this light, is that of *Homo floresiensis* on Flores, a small island hominin of Middle to Late Pleistocene age (Morwood *et al*. 2004, Sutikna *et al*. 2016) and possibly derived from an early dispersal of *Homo erectus* (Brown *et al.* 2004, Morwood *et al.* 2004). Furthermore, several other Pleistocene hominins of uncertain taxonomic affinity are known from Asia. These include the enigmatic red deer cave people from Southern China (Curnoe *et al.* 2012) and the Siberian Denisovans (Krause *et al.* 2010, Reich *et al.* 2010). More indirect evidence for the presence of Middle Pleistocene hominins comes from recent discoveries like Kalinga in the Philippines (Ingicco *et al.* 2018) and Talepu in Sulawesi (van den Bergh *et al*. 2016). The suggestion by these discoveries that the Asian palaeoanthropological record may have been more diverse, has already driven some researchers to question the taxonomic status of some of the Javan *Homo erectus* fossils (Zanolli *et al.* 2019). Further research will, however, have to confirm whether this is in fact the case, but for now I will take the more traditional stance that *Homo erectus* is the only pre-modern hominin present in the Pleistocene of Java.

Morphologically, *Homo erectus* is characterized by a number of novelties compared to its predecessors. Foremost, with 700 to 1300 cc (Dunsworth 2010) its endocranial volume was

substantially larger than that of *Homo habilis* (around 500 cc) (Miller 1990). The Dmanisi crania are an exception in that their capacities are unusually small for this species (600 to 775 cc), although still larger than those of *Homo habilis* (Rightmire 2006, Curran 2009). Furthermore, there is a trend of increasing encephalization from the older to the younger specimens (Klein 1999). The youngest fossils have cranial capacities that approach those of modern humans (Klein 1999). The underlying factors that drove encephalization in *Homo erectus* are still a matter of debate (Shultz *et al.* 2012, Lesciotto & Rightmire 2019), but it is thought that the increase in brain size allowed for the execution of more complex cognitive tasks (Shultz *et al*. 2012).

The cranium of *Homo erectus* typically has a thick browridge that sometimes forms a bony shelf called the supraorbital torus and the frontal bone recedes after the browridge towards the back of the skull (Dunsworth 2010). The overall shape of the cranium is low and elongated, has a strong torus on the occipital bone and often a sagittal keel running from the frontal bone to the top of the skull (Dunsworth 2010). The cranial bones of *Homo erectus* are also thicker than those found in *Australopithecus* or *Homo sapiens* (Kennedy 1991, Dunsworth 2010). Its teeth are relatively small compared to those of earlier forms (Anton 2003).

The postcranial anatomy of *Homo erectus* is less well known due to the lack of fossils from this part of the skeleton. Most of what we know comes from the Nariokotome skeleton (Dunsworth & Walker 2010). Unlike that of *Homo habilis* (Collard & Wood 2015), the skeleton of *Homo erectus* is similar to that of modern humans and consistent with habitual, long range bipedalism (Collard & Wood 2015). Notable differences are that the cortical bone is thicker and that the skeleton is somewhat more robust than in *Homo sapiens*. The shafts of tibia and femur tend to be more flattened in the anterio-posterior plane relative to those of modern humans (Collard & Wood 2015). Adult *Homo erectus* probably stood about 160 cm and may have weighed 50 kg (Dunsworth 2010).

3.4 Archaeology and behaviour

While some earlier evidence for tool making has recently come to light (Harmand *et al*. 2015), it is traditionally assumed that the earliest stone tools were made in Africa by members of the genus *Homo* (Harris 1983a). This early technology, known as the Oldowan industry, is usually associated with *Homo habilis* and dates back to about 2.6 Ma in Ethiopia (Semaw *et al.* 1997).

Homo erectus probably continued using the fairly simple Oldowan technology but some researchers notice a development towards more complexity between 1.8 and 1.5 Ma (Cachel & Harris 1998, Anton & Swisher 2004). It is thought that by 1.5 Ma, *Homo erectus* started developing a more advanced technology, called the Acheulean industry (Haviland *et al.* 2013). As opposed to the less complex pebble technology associated with the Oldowan, the Acheulean industry typically includes more advanced teardrop-shaped handaxes (Haviland *et al.* 2013). This form probably represents the emergence of systematization, predetermination and the idea of symmetry in the archaeological record (Carbonell *et al.* 1999, Barsky 2009).

It was initially thought that the Oldowan was a uniquely African phenomenon and that the Acheulean industry was the first to spread along with *Homo erectus* across larger parts of the old world. More recently this view has been contested (Barsky 2009). A number of Eurasian sites such as Orce in Spain (Gibert *et al.* 1998), Dmanisi in Georgia (Lordkipanidze *et al*. 2013) and Ubeidiya in Israel (Shea 1999) have also produced Oldowan artefacts. Further to the east, Oldowan-like tools are found in Southern Asia (e.g. at Riwat, Pakistan) (Allchin 1981) and increasingly in Chinese sites, like Xiaochangliang and Lanpo (Hong *et al.* 2013).

The Acheulean probably originated in Africa and from there spread to Eurasia (Haviland *et al.* 2013). Artefacts are known from sites such as Saint Acheul (Mortillet 1872) in France and several sites in Asia such as Gilan in Iran (Biglari 2011) and Hungsi and Baichal in India

(Paddayya 2007). From associations between fossils and lithic artefacts at sites such as Koobi Fora (Braun *et al*. 2008) and Swartkrans (Hall *et al.* 2006) it is clear that *Homo erectus* was making Acheulean tools. At other sites where traces of this technology have been found, the association with a specific taxon is less clear and other species such as *Homo heidelbergensis* and *Homo sapiens* may have also produced stone tools of this type (Corbey *et al.* 2016).

In Southeast Asia Early Palaeolithic stone implements are rare (Haviland *et al.* 2013). Before the 1980's there was a consensus that east of the so called Movius line, the Acheulean was absent and that hominins east of this line only made use of more crude flakes and cores and that this was indicative of the less progressive character of their societies (Movius 1944, 1948). This demarcation line, based on Movius' research in Burma (Movius 1944, 1948), extends from the Bay of Bengal, west of the Ganges-Brahmaputra delta, north over the Himalayas and west through Central Asia (Swartz 1980, Brumm & Moore 2012). There are, however, a number of conceptual problems with this model that have led researchers to question the validity of Movius line (Dennell 2009, 2014, 2016, Brumm & Moore 2012). First of all, there is no reason to assume that the presence of bifaces is an indicator of progress (Dennell 2014). It is more likely that their presence or absence is an adaptation to local or regional environmental conditions (Dennell 2016). Moreover, the chronostratigraphic framework and the archaeological evidence on which Movius (1944, 1948) based his research, were flawed (Dennell 2014, 2016). Besides the fact that some of the collected "artefacts" were probably geofacts, there is little evidence that they are contemporaneous with the Middle Pleistocene Acheulean sites of the Middle East or Africa (Dennell 2014). Probably most hominin sites in Southeast Asia are in fact of Late Pleistocene age. So if a clear difference existed between East and West Asia during the Middle Pleistocene, it was more likely one between a more densely occupied West versus a more sparsely occupied East (Dennell 2014, 2016). Some (Brumm & Moore 2012) have argued that this could also be the

result of differences in collection strategy and interpretation and that some bifaces are indeed known from sites in the region such as Ile in the Philippines (Dizon & Pawlik 2010) and Kota Tampan and Kuatan in Malaysia (Collings 1937, 1938). In any case, the original idea by Movius (1944, 1948) of East and Southeast Asia as a backwater in hominin evolution, is questionable.

In Indonesia, stone tool assemblages are generally rare and never found in direct association with pre-modern hominin fossils (Anton & Swisher 2004). The exception, are two assemblages found at Mata Menge and Liang Bua (Flores), linked with *Homo floresiensis* (Brumm *et al*. 2006, 2010). On Java fairly simple flakes and flaked cores have been discovered at Sangiran (Simanjuntak 2001) and at Sambungmacan (Jacob *et al.* 1978). These artefacts are thought to represent a multipurpose, least-effort stone technology that required little advance planning and is probably related to the Oldowan industry (Shea 2006, Brumm & Moore 2012). Besides these stratified finds, a number of Acheulean-like bifaces are reported from surface contexts (Brumm & Moore 2012). At certain localities, such as the Baksoka river bed near Pacitan and at some unspecified sites along the Baksoka River, even relatively high densities have been recovered in the past (von Koenigswald 1936, van Heekeren 1955). Absolute dates for these finds are non-existent (Simanjuntak 2004) and the classification of these artefacts as Acheulean is uncertain (Brumm & Moor 2012). A possible explanation for the scarcity of lithic artefacts in early Indonesian sites may be a preference for other materials for the construction of tools. The recent discovery of some shells from Trinil, with signs of modification by retouch, is in support of this theory (Joordens *et al.* 2014).

Besides lithic artefacts, some *Homo erectus* fossils have been associated with animal remains that show traces of butchery. While the emergence of more persistent carnivory in hominins is thought to have occurred around 2.6 Ma, alongside the appearance of flaked lithic technology, more substantial zooarchaeological evidence presents itself from around 2 Ma (Ferraro *et al.*

2013). Modified animal remains have been found at a number of *Homo erectus*-sites such as Olduvai (Yravedra *et al.* 2016), Koobi Fora (Pobiner *et al.* 2008), Swartkrans (Pickering *et al.* 2004), Zhoukoudian (Boaz *et al*. 2004) and Sangiran (Choi & Driwantoro 2007). While the discussion whether early hominins were mainly hunters or scavengers is ongoing (e.g. Stiner 1994, Pante 2013, Pobiner 2015, Dominguez-Rodrigo & Pickering 2017), most zooarchaeological studies have indicated that *Homo erectus* had primary access to carcass foods (Pickering *et al.* 2004, Pobiner *et al.* 2008, Pante 2013). This is unsurprising as the species distinguishes itself from earlier hominins by its large body size and brain (Wood 1992), anatomical structures with a high metabolic cost that require an increased nutritional intake (Aiello & Wheeler 1995, Pante 2013).

Another novelty that may have appeared for the first time in the archaeological record with *Homo erectus,* is the controlled use of fire. Some evidence from Swartkrans and Koobi Fora could be indicative of controlled fire use from as early as 1.5 or 1.6 Ma (Brain & Sillen 1988, Bellomo 1994). Although these sites fall into the age range of *Homo erectus*, the notion that such traces come from intentional hearths is not uncontested (Attwell *et al.* 2015). Evidence is more compelling for the Middle Pleistocene and sites such as Zhoukoudian (Rolland 2004) and Gesher Benot Ya'aqov in Israel (Goren-Inbar *et al.* 2000) indicate controlled fire was probably well in use by hominins by then (Attwell *et al.* 2015).

In general, archaeological and anthropological data indicate that *Homo erectus* was a social species. Pathological specimens from Koobi Fora (KNM-ER 1808 with extensive periostitis) (Leakey 1974) and Dmanisi (D3444 and D3900 are edentulous) (Lordkipanidze *et al.* 2005) may be indicative of altruistic behaviour, as these individuals could only have survived their conditions with the assistance of their conspecifics (Dunsworth & Walker 2002). Some researchers have suggested that due to *Homo erectus*' bipedal locomotion and increased cranial size, there was a necessity for birth assistance and possibly longer-term assistance

throughout childhood rearing (Rosenberg & Trevathan 1996, Anton 2003). Such life history changes would have involved increased cooperation and perhaps a more important role for postmenopausal females in the upbringing of children (O'Connell *et al.* 1999, Aiello & Key 2002). Although there is no consensus about the appearance of language in hominins (Luke-Killam 2001), some believe that *Homo erectus* had language-like abilities (Wynn 1998).

3.5 Dispersal and palaeoecology

3.5.1 Introduction

There is a significant body of literature available that deals with palaeoenvironmental reconstructions of *Homo erectus* sites. The proxies used for such reconstructions are diverse and range from geomorphology, over palaeobotany, palynology and isotope geochemistry to several subfields of palaeozoology. I follow Bishop and colleagues (2006) and consider the use of multiple proxies in contrast with each other as the most useful way for reconstructing the ecology of an extinct taxon. Section 3.5.2 provides a *status quaestionis* of palaeoenvironmental reconstructions currently available for the principal *Homo erectus* sites. For the purpose of this study I have limited myself to sites where *Homo erectus* (sensu lato) fossils have been positively identified. Sites with merely archaeological remains or with fossils of dubious taxonomic affinity were generally avoided. Section 3.5.3 provides a theoretical framework about *Homo erectus* dispersal and explains how palaeoecology can contribute to our understanding of early *Homo* behaviour in the Pleistocene. This thesis ultimately deals with hominin behaviour and the theories about human dispersal that are discussed in this section will provide a foundation for the hypotheses that are tested in this dissertation.

3.5.2 Palaeoenvironmental reconstructions of *Homo erectus* sites

3.5.2.1 Africa

Palaeoecological data for the Middle Pleistocene sites in North Africa is limited. Moreover the incomplete contextual information available for most of the hominin sites in this region (Raynal *et al.* 2002) hampers new palaeoenvironmental reconstructions. Nevertheless, the palaeoecological signature of "Rhinoceros cave", a site close to- and contemporary with-Thomas Quarries has provided some insight (Geraards 1980, 1993, 1994). Rich collections of fossil mammals, including large numbers of gerbillids, alcelaphines and gazelles, suggest an open, dry environment for the Middle Pleistocene levels (Geraards 1980, 1993, 1994). A similar fauna was observed at Ternifine (Geraards *et al*. 1986), but in the latter case *Hippopotamus* suggested the presence of open water, probably subject to regular drainage given the absence of fish or crocodile. The palaeoenvironment was described as an open, arid landscape surrounding a seasonal lake or swamp (Geraards *et al.* 1986). At Sidi Abderrahman gerbillids were also predominant (Raynal *et al.* 2002). An analysis of carbon and oxygen isotopic signatures from mammal teeth from Ternifine confirmed the pattern described from the palaeozoological analyses. None of the mammal remains had very low δ13C values, typical for forest dwelling species, suggesting an open environment (Bocherens *et al.* 1996).

A lot of what is known about *Homo erectus* palaeoecology comes from the East African palaeoanthropological sites. Olduvai in northern Tanzania has seen extensive fieldwork and many projects have included palaeoenvironmental reconstructions (e.g. Shipman & Harris 1988, Sikes 1994, Bonnefille 1984). The Upper Beds (II) of Olduvai Gorge, relevant to *Homo erectus* have, however, been comparatively neglected. Nevertheless, some data is available. Several authors (Gentry & Gentry 1978, Shipman and Harris 1988) have pointed out that the species composition (mainly of bovids) indicate the presence of a diverse range of habitats,

but that the younger layers with *Homo* are typically rich in Antilopini and Alcelaphini, suggesting drier, more open habitats, perhaps equivalent to dry open bushland or tree savannah plains (Gentry & Gentry 1978, Shipman & Harris 1988). Shipman and Harris (1988) noted that there may have been a gradual trend towards aridification from the oldest, Pliocene layers (containing *Australopithecus*) to the younger Pleistocene strata (containing *Homo*). Based on these findings it was concluded that members of the genus *Homo* were able to cope with a wider range of habitat types and, unlike the robust australopithecines, were able to use drier, more open habitats (Shipman and Harris 1988). Although ecomorphological studies on bovid postcranial elements have mainly focused on the older Bed I strata, several analyses (Kappelman 1984, 1997, Plummer & Bishop 1994) have also indicated a gradual aridification of the landscape towards the end of Bed I.

Furthermore, this trend towards increasingly arid habitats in the Upper Beds of Olduvai (II, III and IV) seems to be corroborated by geological data. In Bed II evidence has been described for the occurrence of flash flooding and mudflows, indicative of a (semi-) arid climate with regular downpours (Hays 1976). There were also indications for shorter climatological episodes within Bed II when conditions became even drier. In the upper parts of Bed II there was probably little standing water left (Hays 1976, Bishop 1994) and the Olduvai palaeolake may have at times completely disappeared (Ashley *et al.* 2010a). Palynological analyses have confirmed this picture. The Bed II sediments are generally characterized by an arid species spectrum and are interpreted as steppe-like grassland or wooded grassland (Bonnefille 1984, Ashley *et al*. 2010b). In addition there were indications for a very dry episode at the transition between Bed I and II (Bonnefille 1984).

Some have nevertheless questioned this model of an increasingly arid environment. Kovarovic and colleagues (2013) have argued that the ecological differences extrapolated from species composition and from sedimentological analyses may have been overstated.

Based on a quantitative palaeoecological analysis of the mammal remains they acknowledge the existence of a climatic shift resulting in the disappearance of the Olduvai palaeolake, but warn for oversimplification and that taphonomic factors may play role in the faunal composition (Kovarovic *et al.* 2013). The results of a reanalysis of old finds in combination with new fieldwork have recently also indicated that a more wooded environment may have been present in the area than originally thought (Dominguez-Rodrigo *et al*. 2010).

The area around Lake Turkana has also provided valuable insights into the palaeoecology of *Homo erectus*. Especially Koobi Fora (East Turkana), the oldest *Homo erectus* site, is important as it may provide a baseline for the type of habitat in which this species originally evolved (Curran 2009). As in this area of East Africa large numbers of vertebrate fossils have been discovered and especially bovids have played a prominent role in palaeoenvironmental reconstructions here (Harris 1991, Bobe *et al.* 2007, Bobe 2011). Faunal analysis has indicated a relatively high degree of heterogeneity at different areas of the Turkana basin (Bobe *et al*. 2007, Patterson *et al.* 2017a, 2017b). At Omo, conditions were relatively wet and wooded for much of the Plio-Pleistocene (Bobe *et al.* 2007). West Turkana, on the other hand, had large proportions of Alcelaphini, Antilopini and Hippotragini in the taxonomic spectrum, tribes indicative of open and seasonally arid grasslands. The conditions at East Turkana were probably intermediate between those found at Omo and West Turkana (Bobe *et al.* 2007) and may have supported lake margin- and riverine environments (Behrensmeyer *et al.* 2016). Ecomorphological studies on bovid fossils seem to confirm this diversified picture, but general conditions were suggested to have been more wooded than at Olduvai (Kappelman *et al.* 1997, Plummer *et al.* 2015). An analysis of micromammal assemblages suggested on the other hand relatively dry conditions, but with the presence of riverine forest (Denys 1999).

Similar to the fauna at Olduvai, the fauna at Turkana also seems to be indicative of a gradual aridification of the landscape during the Plio-Pleistocene. Around 2 Ma new, open adapted,

bovid species appear in the fossil record, as well as the less arboreal primate *Theropithecus oswaldi* (Bobe 2011). The browsing proboscid *Deinotherium* disappears on the other hand (Harris 1983b, Bobe 2011). These changes have usually been correlated with the expansion of grassland during this period (Bobe 2011). A recent quantitative analysis of the mammalian fauna (Fortelius *et al.* 2016) indicated a possible decrease in precipitation from 1000 to less than 500 mm/year in the last six million years, but relatively stable temperatures around 24°C. According to the authors this could reflect a balance between a globally cooling climate and local heating due to decreasing forest cover and the increased prevalence of grassland (Fortelius *et al.* 2016). It was also suggested that the Turkana Basin, during certain episodes, may have acted as a refugium due to the presence of the Omo River, but that for most of the Plio-Pleistocene it was probably even more arid than the surrounding area. This situation would make Turkana an ideal location for new hominin species to arise that were (pre)adapted to local (arid) conditions and were eventually to spread over larger areas (Fortelius *et al.* 2016).

Geomorphological and geological studies have shown that the depositional environment at Koobi Fora was characterized by a succession of floodplain systems interspersed with lacustrine phases during which the basin was largely flooded (Feibel 1993, Patterson *et al*. 2017b). Between 2 and 1.8 Ma a lacustrine environment was present, succeeded by a regression of the lake and replacement with fluvial depositions from riverine environments from 1.8 to 1.7 Ma (Feibel 1993, 2011). In the proximity of the Omo River, gallery forests would be supported, while further away the landscape would be dominated by dry scrubland (Feibel 1993, 2011). Stable carbon isotopes from pedogenic carbonates have suggested a landscape during this period with vegetation ranging from wooded scrubland to grassland (Quinn *et al*. 2013, Patterson *et al.* 2017b). An analysis of carbon isotopes in stromatolites

from East Turkana has indicated a climatic evolution from fairly wet, cool conditions before 1.9 Ma, to drier, warmer conditions around 1.4 Ma (Abell *et al.* 1982).

Palynological analyses have also evidenced the fluviatile and lacustrine character reconstructed from geological data (Bonnefille 1976). Pollen spectra for the period between 2.5 and 2 Ma have revealed a fairly open landscape with a mosaic character and patches of grassland. Near the river, more wooded vegetation must have been present. A trend towards more open landscapes was observed. By 2 Ma, the region was apparently covered by a savannah with few trees, reflecting drier conditions than before (Bonnefille 1976). This trend seems to continue and by 1.88 Ma, the pollen record points towards a cooler, drier landscape with bushland, gallery woodland and grasslands (Vincens 1982).

Palaeoenvironmental proxies at Olorgesaillie provide some insight into the palaeoecology of *Homo erectus* at a later stage of the Pleistocene in East Africa (aprox. 0.9 Ma) (Potts *et al*. 2004). Geological studies have demonstrated that diatomite depositing lakes and wetlands were apparently predominant throughout the Olorgesaillie formation (Behrensmeyer *et al.* 2002, Owen *et al*. 2008). This palaeolake environment was associated with alternating freshwater and slightly saline wetland phases (Behrensmeyer *et al.* 2002, Kübler *et al.* 2015).

In Ethiopia additional data is available from a number of sites. At Melka Kunture the mammalian palaeoecological signature, especially based on the bovid spectrum, is interpreted as dry and open with the dominance of antilopines and alcelaphines and the lack of reduncines and tragelaphines (Geraards *et al.* 2004). Moreover, as most identified mammals are specifically or sub-specifically distinct from contemporary forms found in Kenya and Tanzania, Geraards and colleagues (2004) interpreted this as the result of a geographical isolation of this part of Ethiopia from the rest of East Africa during the Pleistocene. The results of an isotopic analysis of mammalian teeth indicated mammals were mainly relying on

a diet of C4 plants, similar to that found in modern grazers of open environments (Bocherens *et al.* 1996). A study of the micromammals revealed almost exclusively the presence of the molerat *Tachyoryctes* in Early Pleistocene layers, a genus typical of savannah-like environments or high altitude steppes (Sabatier 1982). In the Middle and Late Pleistocene layers this predominance was also noted, but enriched with other taxa, such as *Stenocephalemys* and *Oenomys*, associated with extant habitats in Ethiopia at high altitudes and forest-steppe ecotones (Sabatier 1982). The presence of Anatidae (ducks or geese) suggest the presence of a swamp or open water reservoir (Pichon 1979). Palynological research has demonstrated that grasses were an important component of the Melka Kunture ecosystem throughout the Quaternary, indicating an overall open environment, perhaps best classified as open woodland or highland shrub (Bonnefille 1972). Especially in the Early Pleistocene, open environments were predominant. In the Middle and Late Pleistocene some forest cover must have been present (Bonnefille 1972).

Additional data is available from the Middle Awash valley. Palaeontological studies at Bodo have indicated the presence of terrestrial taxa requiring grasslands (e.g. *Onotragus, Equus*) as well as aquatic forms (e.g. *Crocodilus* and *Hippopotamus*) indicative of a water reservoir (Kalb *et al*. 1980). Amongst the vertebrate fossils from Bouri, alcelaphines were the dominant bovids, suggestive of open grassland. A few *Kobus* specimens and the presence of *Hippopotamus* pointed to the existence of water-margin habitats in the vicinity (Asfaw *et al.* 2002). Pollen remains are not well preserved in this part of Ethiopia, but preliminary phytolith analyses on samples from the western Middle Awash have indicated that Pleistocene environments were probably dominated by grassland with scattered woody elements. C4-grasses appear to have been an important component (Barboni *et al*. 1999). Carbon and oxygen isotopes from palaeosols and mammalian teeth have indicated that samples associated with *Australopithecus* around 2.5 Ma corresponded with dry wooded grassland, but that

younger samples (around 1 Ma) associated with *Homo* reflected drier, more open conditions (Ambrose *et al.* 2016). A trend towards increasingly dry landscapes, as was observed in Kenyan and Tanzanian sites, may therefore also have occurred in this part of Ethiopia.

In South Africa several sites have yielded fossils identified as *Homo* sp., but only the remains from Swartkrans have been positively attributed to *Homo erectus* (Rightmire 1990). As such, my review of this region will be limited to data from Swartkrans. Palaeozoological research has demonstrated that over the course of the last 2 million years, alcelaphines were the dominant bovid tribe at this cave site. This would imply that regional landscapes were characterized by open environments and grasslands (Vrba 1975). Possibly the younger strata at Swartkrans were more arid than the older ones (Vrbra 1975). This picture was further corroborated by analyses of the micromammals, pointing to open grassland, with woodland on the riverside (Avery 1995). A study of the primates has on the contrary suggested the presence of closed woodland as the main vegetation in the area (Benefit & McCrossin 1990).

The predominance of open environments and an evolution towards increased aridification in this area is nevertheless supported by isotopic studies on fossil tooth enamel. A trend towards more open environments was observed from 3 Ma, with a marked change to open grassland around 1.7 Ma (Lee-Thorp *et al.* 2007). Well preserved pollen samples are absent from Swartkrans and most other sites in the area, but some preliminary data may suggest that the transition between the older strata, containing *Australopithecus*, and the younger strata with *Homo*, could have occurred in an open savannah environment (Scott & Bonnefille 1986).

3.5.2.2 East and West Asia

The palaeoecology of Dmanisi, the primary site of interest in Western Asia, is relatively well studied. The vertebrate fauna contains representatives of a range of habitats, but forest-steppe taxa, such as *Ochotona* and *Struthio*, are an important component of the assemblage (Gabunia

et al. 2000a). A high diversity of cervids is thought to reflect the vertical zonality of the nearby forested mountains and species like *Dama* cf. *nesti* are assumed to have had a preference for more open habitat (Gabunia *et al.* 2000a). Indicators for the presence of forested zones in the area may be found in fossils of artiodactyls such as *Soergilia*, *Eucladoceros* and *Dmanisibos* (Gabunia *et al.* 2000a). Overall the spectrum is suggestive of a mixed mosaic environment with open landscapes, gallery forest along the river valleys and forested mountains (Gabunia *et al.* 2000a). The herpetofauna from the site point to a warm, dry climate and an arid steppe-like vegetation (Blain *et al.* 2014). Steppe-like conditions are also evident in the micromammal fauna (e.g. *Gerbillus* sp.) and in preliminary data on the malacofauna (Gabunia *et al.* 2000a).

The results of a palaeobotanical and palynological analyses confirm the reconstructions based on the palaeozoological record of Dmanisi. The macrobotanical remains indicate a temperate climate and an open vegetation dominated by grasses (Messager *et al*. 2010). The pollen spectrum suggests the presence of some (possibly riparian) forest in the region. The environment at Dmanisi is suggested to have been similar to the environments that *Homo erectus* occupied in East Africa during the Early Pleistocene (Messager *et al.* 2010). Possibly the palynological record also suggests increasingly arid conditions at the time of deposition (Gabunia *et al.* 2001). This is in line with palaeobotanical evidence from elsewhere in Georgia, indicating an aridification and reduction of forest cover from the end of the Pliocene (Shatilova & Ramishvili 1990, Gabunia *et al*. 2000a).

Much less has been published about the palaeoecology of the Kocabas hominin from Turkey. The mammal remains are difficult to study as they are embedded in the thick travertine matrix from where the human skull fragment also came. Generally speaking, the palaeoenvironment is thought to be characterized by abundant freshwater and swamp vegetation, surrounded by dry limestone hills (Lebatard *et al.* 2014).

Of the Chinese *Homo erectus* sites Zhoukoudian (Locality 1) is probably the best studied. This Middle Pleistocene site, containing rich sequences of lithic artefacts, animal and human remains (Dennell 2009), provides most relevant palaeoenvironmental data about the region. The age of the large number of hominin remains discovered there is uncertain, but can probably be placed somewhere between 400 and 600 Ka (Zhu & Zhou 1994, Shen *et al*. 1996, Zhou *et al*. 2000, Dennell 2009). The mammalian record is quite rich and primarily dominated by cervids, rhinoceros and a large number of carnivore remains (Pei 1934, Aigner 1981, Dennell 2009). Depending on the layer, the fauna is either indicative of a more open (e.g. layers 8-9 and 10), or more closed (e.g. layer 4) forest-steppe environment (Li & Ji 1981, Zhu & Zhou 1994). Evidence from carbon and oxygen isotope analyses of cervid tooth enamel has pointed to a mixed combination of C3/C4 plants in the older layers (Gaboardi *et al.* 2005). The amount of C4 vegetation is thought to have decreased from the beginning of the Middle Pleistocene up until 470 Ka, perhaps related to a strengthening of the winter monsoon over that time period (Gaboardi *et al.* 2005). A number of bird remains have been reported from Zhoukoudian and the record is dominated by species of dry environment, including steppe forms such as *Struthio* and *Aquila heliaca* (Wu & Poirier 1995, Hou & Zhou 1999). A study of the micromammals from Zhoukoudian has pointed out an increase of dry-adapted rodents from the older to the younger layers. The region was at least in the early phases probably dominated by grasslands (Jin *et al*. 1999).

Despite low pollen incidence in most samples, some attempts have been made at inferring palaeonvironmental data from palynological analyses at Zhoukoudian (see Della Croce 1995 for an overview). An early attempt on a small sample has indicated low numbers of non-arboreal pollen with a dominance of *Pinus*, *Betula* and *Picea*, suggesting a border zone between the temperate steppe and northern conifer forests (Kurten & Vasari 1960). Later palynological studies have demonstrated differences between individual stratigraphic layers.

The presence of a broadleaf-conifer mixed forest with grasslands in layer 10, suggested a temperate climate much like that of today (Liu 1985b), while in layers 8 and 9 the spectrum was characterized by an increase in taxa typical of broadleaf-forest. This was probably related to an increase in temperature (Liu 1985b, Zhu & Zhou 1994). The contents of Layer 4 were suggestive of a mixed broadleaf-conifer forest with shrub/steppe again (Zhu & Zhou 1994). The results of a study by Kong and colleagues (1985) indicated interglacial conditions in layers 9, 8, 6 and 4, and open, colder conditions in layers 11, 10 and 7.

From the Xujiayao hominin site Middle and Late Pleistocene fluviatile and lacustrine sediments are availablewith animal remains indicating temperate and cold conditions (Chia *et al.* 1979, Wu & Trinkaus 2014). Geomorphological data has suggested somewhat cold environments for this site (Li *et al.* 2016), an observation confirmed by limited palynological evidence (Wu & Trinkaus 2014). In addition, palaeoecological data is available from a number of archaeological sites from the Nihewan Basin, including Donggutuo, Xiaochangliang and Majuangou. Pollen data is available from Donggutuo (Pei *et al.* 2009). Although no hominin fossils were found there, the archaeological record and chronology (around 1.1 or 1.2 Ma) (Wang *et al*. 2005, Pei *et al.* 2009) are compatible with the cultural and temporal range of *Homo erectus*. Human presence was attested in the earliest sequences of the site, corresponding with three environmental stages, based on the pollen spectrum. The earliest stage is indicative of warm and humid forest-steppe, changing in a second stage to drier, more temperate forest steppe. In a third stage, conditions became more warm and humid again (Pei *et al.* 2009). The mammal remains at this site were in a highly fragmented state, complicating identification, but the faunal spectrum is in line with a forest steppe interpretation, confirming the palynological analyses (Pei *et al.* 2009). A fossil record typical of the Nihewan beds is represented at Donggutuo, including rhinoceros, cervids, bovids, proboscids and a predominance of equids (Schick *et al.* 1991).

Evidence is also available from another archaeological site in the Nihewan basin: Xiaochangliang. This assemblage is dated between 1.6 to 0.9 Ma according to Peterson et al. (2003). Others have specified its age around 1.36 Ma (Zhu *et al.* 2001), or even 1.67-1.78 Ma (Tang *et al.* 1995). The highly fragmented vertebrate remains from this site include a range of forms such as *Equus, Palaeoloxodon, Hipparion, Coelodonto, Cervus, Gazella* and *Struthio* (Peterson *et al*. 2003, Dennell 2012). Assuming these remains are of the same age as the lithic artefacts, the conditions met by the hominins were probably those of a temperate, semi-arid steppe environment (Dennell 2012). In an isotopic study of equid enamel an important signal of C3 plants was found throughout the Pleistocene layers at this site (Wang *et al*. 1998).

At Majuangou (III), also in the Nihewan Basin and estimated around 1.66 million years old (Zhu *et al.* 2004), malacological and palaeobotanical remains suggest the presence of a fairly warm climate and the presence of a marsh environment (Zhu *et al*. 2004, Dennell 2012). The vertebrate record includes a range of forms, such as cervids, equids, several carnivores, steppe mammoth (*Mammuthus trogontherii*) and *Struthio*, most of which are indicative of warm, steppe-like conditions (Zhu et al. 2004, Keates 2010).As far as Gongwangling is concerned, the human and animal remains were discovered at the bottom of a weakly developed palaeosol in a silt layer (Zhu & Zhou 1994), for which more recently a date of 1.63 Ma has been proposed (Zhu *et al.* 2015). The silt layer is associated with a cold and dry climate, while the bordering palaeosol, reflects warm and humid conditions (Zhu & Zhou 1994). The *Homo erectus* remains mainly originate from the transitional phase between these warm and cold episodes (Zhu & Zhou 1994). The mammal remains are suggested to be similar to the *Stegodon-Ailuropoda* assemblages (Zhu & Zhou 1994), typical for the south of China (Kahlke 1961). The mandible from Chengjiawo (also Lantian) was found amongst mammal fossils associated with steppe environments (Zhu & Zhou 1994). A palynological analysis specified that it probably concerned a forest-steppe (Wu *et al.* 1989, Zhu & Zhou 1994).

3.5.2.3 Southeast Asia

The hominin fossils at Trinil were found in fluviatile deposits that were part of the ancestral Solo River system. The physiographic circumstances around the site are thought to have been similar to those found in the area today (Huffman 1997, 1999). Palaeoecological reconstructions of Trinil have been mainly based on the vertebrate fauna, but interpretations have at times been contradicting. In early work (Selenka *et al.* 1911) Trinil was reconstructed as a forested environment. Although some researchers (e.g. Pope 1995, Louys 2007) still follow this interpretation, more recent reconstructions have inferred an open woodland environment, mainly based on the large amounts of proboscids, bovids and cervids (de Vos *et al.* 1994, van den Bergh *et al*. 2001). Micromammals are rare in the Early and Middle Pleistocene record of Java. Nevertheless some murids found at Trinil are in agreement with an interpretation as open woodland (Van der Meulen & Musser 1999). A small sample of bird remains, including adjudant (*Leptoptilos*), stork (*Ephippiorhynchus*) and some ducks (Anseriformes), indicate a relatively open environment with a wet component (Meijaard 2003a, Joordens *et al*. 2009, Meijer 2014).

Certain re-analyses of the existing palaeozoological data have on the other hand led to different interpretations. Louys' (2007) quantitative approach to study the community ecology of the Pleistocene mammals from Trinil suggested a closed environment. Another re-analysis based on the vertebrate and invertebrate spectrum concluded that the fauna consists of a combination of terrestrial and aquatic taxa and provides a more diversified reconstruction for the Trinil palaeoenvironment, consisting of lowland tropical rainforest, grasslands, floodplains, swamps and rivers (Joordens *et al.* 2009). Ecomorphological studies on bovid postcranial elements have suggested a more open environment, perhaps dominated by grassland, but with densely vegetated river valleys and upland forests (Weinand 2005, Arif & de Vos 2011). An analysis of strontium isotopes from mollusk remains has indicated the

presence of brackish water, possibly reflecting estuarine conditions (Joordens *et al.* 2009). Carbon and oxygen isotopes from ungulate enamel were suggestive of a diet relying primarily on C4 grasses in cervids and most bovids. The diet of the suid *Sus brachygnathus* fell into the C3 range, and indicated the presence of this type of vegetation as well (Janssen *et al.* 2016). No pollen records are known from Trinil.

The palaeoenvironmental conditions at Kedung Brubus are not well known. The fauna from this site is thought to be associated with a peak in glacio-eustatic sea level changes, probably resulting in an extreme sea level drop (Sondaar 1994, van den Bergh *et al*. 2001).The fossils were probably deposited during a glacial maximum (Musser 1982, Meijaard 2003a). The fauna is reconstructed as dry, open woodland, mainly based on the predominance of bovids and the absence of primates (de Vos *et al.* 1994, van den bergh *et al.* 2001). An ecomorphological analysis of some bovid fossils from this site (Weinand 2005) confirmed this interpretation and suggested that at Kedung Brubus conditions may have been drier than at Trinil. The Kedung Brubus fauna may have seen a reduction of the upland forests and closely vegetated river valleys that were present in the Trinil (H.K.) phase (Weinand 2005). Louys' (2007) reconstruction of the community ecology of the site, on the other hand, classified Kedung Brubus as a closed, forested environment.

The palaeoenvironments of Sangiran have been comparatively well studied. At this site four formations are exposed, from old to young: the Kalibeng (or Puren) formation, the Pucangan (or Sangiran) formation, the Kabuh (or Bapang) formation and the Notopuro (or Pohjajar) formation (Indriati & Anton 2008).Together they cover a temporal range between 2.6 and 0.2 Ma (Bouteaux 2005). The Kalibeng Formation is composed of marine deposits (Indriati & Anton 2008). Most terrestrial fossils are found in the Kabuh formation (Indriati & Anton 2008), that is separated from the older and less rich Pucangan formation by a conglomerate layer called the Grenzbank (Bouteaux 2005). The oldest *Homo erectus* remains come from the

upper levels of the Pucangan Formation (Indriati & Anton 2008), the youngest from the upper Kabuh Formation (Bouteaux 2005). The exact age of the Kabuh and Pucangan formations and their (bio)stratigraphic correlation with other sites from Java is still a matter of debate (Indriati & Anton 2008, Matsu'ura *et al*. 2020), but it is thought that the lowest part of the Kabuh formation and the Grenzbank can be correlated with the Trinil (H.K.) fauna (0.8-0.9 Ma) and the upper Kabuh formation with the Kedung Brubus fauna (0.7-0.8 Ma) (van den Bergh *et al*. 2001, Bouteaux 2005). The Pucangan formation can probably be correlated with the Early Pleistocene Satir and Ci Saat faunal units (Bouteaux 2005). As such the formations at Sangiran are associated with different depositional histories and probably varying environmental conditions that changed through time (Bettis *et al.* 2009).

For the Pucangan formation, geological research has indicated that the upper levels were composed of black clay deposits, including siltstone and mudstones accumulated in brackish water, lacustrine environments and marshes (Watanabe & Kadar 1985, Bettis *et al.* 2009). A change from standing water to more fluvial environments marks the transition from the Pucangan to the Kabuh formation (Watanabe & Kadar 1985, Bettis *et al*. 2009). The latter consisted primarily of cross-bedded sandstones and pebbly sands (Indriati & Anton 2008). A similar picture was provided by palaeosol analysis, with pedotypes in line with a poorly drained landscape along lake or marsh margins in the Pucangan formation. Size and density of root traces also provided some evidence for the presence of shrubs with shallow rooted grasses and ferns (Bettis *et al.* 2009). Palaeosols in the Kabuh formation on the other hand, were better drained due to fluvial conditions and also showed root traces and bioturbation. Open woodland conditions were probably present during this phase (Bettis *et al.* 2009).

The vertebrate fauna from the Pucangan formation is not well known, but was probably an endemic island fauna, with animals typical of marshy and lacustrine environments such as crocodile and hippo (*Hexaprotodon*) (Aimi & Aziz 1985, Bouteaux 2005). This would be in

line with the interpretation of the Pucangang formation as a Satir and/or Ci Saat fauna sensu de Vos and Sondaar (de Vos & Sondaar 1982, de Vos et al. 1982, 1994, de Vos 1985, Sondaar 1984). Van den Bergh and colleagues (2001) suggested a mangrove-like environment for Satir and Ci Saat. More is known about the palaeozoological record of the Kabuh formation. In general the fauna in this formation appears to be indicative of an open woodland environment, drier than that found in the Pucangan formation and reminiscent of Trinil (H.K.) (Moigne *et al.* 2004b, Bouteaux 2005). Common elements are bovids, cervids and proboscids (Bouteaux 2005). This similarity to the purported open environment found at Trinil was also confirmed by the micromammal record. The spectrum is mainly composed of grassland-adapted murids (Van der Meulen & Musser 1999). An isotopic study (Janssens *et al.* 2016) of fossil tooth enamel showed that bovids and cervids from Sangiran had a predominantly C4 grazing signal, suggesting a dry, open landscape. Suids had either low or high δ13C values, but consistently low carbon isotope values, implying the presence of some closed vegetation as well (Janssens *et al.* 2016). It should however be mentioned that in the latter study, it was unclear whether the samples came from the Kabuh or Pucangan formation (Janssens *et al*. 2016).

Palynological records available for Sangiran allow for a more complete reconstruction of the environmental changes that took place in the Early and Middle Pleistocene. Samples taken from sediments of the Pucangan formation point to the existence of extensive mangroves and swampy tropical forests (Sémah *et al.* 2010, Sémah & Sémah 2012). Within this formation smaller scale changes coinciding with glacial cycles must have resulted in recurring contractions of closed forest to higher altitudes, but fragmentation was limited (Sémah *et al.* 2010, Sémah & Sémah 2012). These circumstances changed in the Grenzbank levels and the Kabuh formation, which appear characterized by an open vegetational cover with seasonal forest rapidly evolving into a more grassland-dominated landscape (Sémah *et al*. 2010).

Forests did not disappear but underwent significant fragmentation, sometimes resulting in locally humid conditions (e.g. at riverbeds) (Sémah *et al.* 2010).

Palaeoecological data for other hominin sites in Java is fragmentary and often difficult to assess due to the uncertainty about the provenience of many of the (hominin) fossils. One such controversial site is Mojokerto. Although efforts have been made to retrace the original find's location (Huffman *et al.* 2005), the exact age and stratigraphic position are still debated (see Morwood *et al*. 2003, Anton & Swisher 2004, O'Connell & Desilva 2013, Ayala & Cela-Conde 2017, Matsu'ura *et al.* 2020). Analysis of a pollen sample that came from the strata where the skull was supposedly discovered, suggested an environment characterized by mangroves and swamps, with forests at higher altitudes (Huffman & Zaim 2003). Some surface finds of vertebrate fossils from the proximity of the site were also typical of a lacustrine or swamp environment (Huffman & Zaim 2003).

Although the provenience of the Ngandong hominins is not well known either (Huffman *et al.* 2010), some vertebrate remains from this site have been briefly described in the literature. The lack of forest fauna is conspicuous at this site (Huffman *et al*. 2010) and the Ngandong palaeoenvironment has been provisionally reconstructed as open woodland, similar to that of Kedung Brubus (de Vos *et al.* 1994, van den Bergh *et al.* 2001).

3.5.3 Dispersal and palaeoecological implications

A unique aspect about *Homo erectus* is that it is generally believed to be the first hominin that expanded outside of Africa into Eurasia (Anton 2003, Anton & Swisher 2004, Leakey & Werdelin 2010). When this early dispersal event (Out of Africa I) took place and which circumstances or adaptations led *Homo erectus* to broaden its biogeographical distribution, are still heavily debated questions (see e.g. Dennell 2001, 2009, Anton & Swisher 2004, Dennell & Roebroeks 2005, Leakey & Werdelin 2010, Carotenuto *et al.* 2016, Medin *et al.*

2019, Herries *et al*. 2020, Matsu'ura *et al.* 2020) and form an important theme in this dissertation. In order to provide an answer to these questions it is vital to first discuss and define dispersal as a biological process.

A distinction should be made between ecological dispersal and biogeographic dispersal (Decae 1987). According to Gibbs and colleagues (2009) ecological dispersal is the movement of animals among local populations and into new areas in the context of landscape fragmentation and climate change, resulting in gene flow. In ecological dispersal this implies a dispersal event within the lifetime of an individual for example for reproduction (Ronse 2007). Such movements may be proximately beneficial for a number of reasons such as reduced competition or avoidance of inbreeding (Ronse 2007). In palaeontology and biogeography, on the other hand, the term is often meant as a wider process where species expand their biogeographical range, perhaps over the course of multiple generations (Pielou 1979, Decae 1987, Lieberman 2005). While ecological dispersal can be part of biogeographic dispersal, it is primarily the latter definition that is relevant to this dissertation.

Biogeographic dispersal is generally subdivided into three different types: jump dispersal, diffusion and secular migration (Pillou 1979, Decae 1987). Jump dispersal is a range expansion induced by the movement of an animal over a large distance followed by the establishment of a new isolated population there (Pillou 1979). Diffusion is the movement of a species into a new area bordering the original range within a limited number of generations (Pillou 1979). Secular migration is a range expansion over the course of many generations often related to evolutionary or long term geological or environmental changes (Pillou 1979). All three forms of biogeographic dispersal may be relevant to early hominin dispersal, but the questions about *Homo erectus* range expansion that will be addressed here, mainly deal with its dispersal on a multi-generation scale in the sense of secular migration. This term should not be confused with migration in the ecological sense, implying seasonal movements of an

individual to and from a certain area (Tchernov 1992, Ronce 2007). Hence I will from here simply use the term (biogeographic) dispersal in this dissertation.

As far as *Homo erectus* is concerned, a few decades ago it was widely believed that this species, after its first occurrence at Koobi Fora around 1.8 to 1.9 Ma (Leakey & Walker 1976), slowly spread to other parts of Africa and the Levant and eventually further into East- and Southeast Asia (Anton & Swisher 2004). In this model, also dubbed the "short chronology", the earliest occupation outside of Africa did not take place until about 0.8 Ma (Klein 1999, Langbroek & Roebroeks 2000, Roebroeks 2001). Some older archaeological evidence from Ubeidiya (Israel) (Klein 1999, Belmaker *et al.* 2002) was dismissed as merely the result of a brief, but temporary incursion in the Middle East and that it was not before the advent and spread of the Acheulean technology that *Homo erectus* was allowed to disperse over larger parts of the Old World (Anton & Swisher 2004).

The "short chronology" was disproved as increasingly robust evidence for an earlier dispersal into Eurasia came to light. Even though not all these early dates are universally accepted, sites such as Dmanisi (1.78-1.85 Ma) (Ferring *et al.* 2011) and Sangiran (1.6 Ma) (Swisher *et al.* 1994, Indriati & Anton 2008, Matsu'ura *et al.* 2020) have convincingly demonstrated that *Homo erectus* was present outside of Africa well before 0.8 Ma. As the chronology of these sites is generally deemed reliable and based on several lines of evidence (e.g. stratigraphic, anatomical, radiometric, palaeomagnetic) many workers (Gabunia *et al.* 2000b, Larick *et al.* 2001, Vekua *et al.* 2002, Anton & Swisher 2004) now accept a "longer chronology" (Anton & Swisher 2004).

Another point of debate is how and by what route *Homo erectus* spread over the Old World. In order for a species to expand its biogeographical range over a larger area it is important that certain conditions are met. In general this means that there must be a physical connection

between the source area and the new region in the form of a corridor or land-bridge (Curran 2009). Nevertheless, various reports exist of human and non-human primates 'jump dispersing' across sea gaps by means of (natural) rafts (Smith 2001). While early *Homo sapiens* probably reached Australia by such means, it is not clear if *Homo erectus*, or any other pre-modern hominin, was capable of crossing larger expanses of water (Smith 2001). The presence of Middle Pleistocene hominins on Flores (*Homo floresiensis*) (Morwood *et al.* 2004) and possibly also on Sulawesi (van den Bergh *et al*. 2016) and the Phillipines (Ingicco *et al.* 2018) seems to suggest so. As these three island regions were probably isolated from the Sundashelf by a deep sea channel since before the beginning of the Pleistocene, they could only have been reached by water (Smith 2001). Others (Kitchener *et al*. 1990) have on the other hand argued that at the beginning of the Middle Pleistocene land-bridges existed that connected at least some of these regions to Sundaland, during episodes of particularly low sea levels. Whether or not some early hominin dispersal happened through rafting is difficult to verify, but it seems plausible that if such movement occurred, it was restricted to points where land masses were at most separated by relatively narrow sea gaps.

What is better known, is that after leaving its home base in sub-Saharan Africa, *Homo erectus* entered North Africa quite soon. Archaeological evidence at Aïn Hanech (Algeria) has indicated that its spread into this part of the continent may already have occurred around 1.8 Ma (Sahnouni *et al*. 2002), followed quickly by occupations in the Levant (Ubeidiya) (Belmaker *et al.* 2002) and Transcaucasia (Dmanisi) (Lordkipanidze *et al.* 2013). This would imply that the North African occupation was probably part of the same dispersal movement that led to the occupation of Eurasia (Lahr 2010). Four potential routes (Fig. 3.2) may have been used by *Homo erectus* to enter Eurasia from Africa: the Strait of Gibraltar (Alimen 1975, Straus 2001), the Sicilian Channel (Alimen 1975), the Bab-El-Mandab Isthmus (Nikitas & Nikita 2005) and the Sinaï Peninsula (Tchernov 1992). The latter route is thought to be the

most likely as it is the only one that was continuously connected to the Eurasian landmass since the Miocene (Tchernov 1992). The spread of *Homo erectus* further east is not well documented, but the species is found relatively early in East and Southeast Asia at sites such as Sangiran (1.6 Ma) (Matsu'ura *et al*. 2020), Gongwangling (Zhu *et al.* 2015) and Zhoukoudian (early Middle Pleistocene) (Rightmire 1991).

Despite advances in our understanding of the timing and route of initial hominin dispersal, the nature of this event remains poorly understood and is surrounded by a number of questions: Why did it happen at this particular time? Why was *Homo erectus* apparently the only species to expand over such a large area as opposed to other contemporaneous and earlier hominins? Was this part of a wider dispersal event including a range of different species? What was the role of climatic and environmental changes (Leakey & Werdelin 2010)? A number of hypotheses have been proposed that attempt to provide answers to these questions.

The general consensus is that the first dispersal of the genus *Homo* out of Africa was initiated by a combination of intrinsic- (i.e. morphological and/or behavioural novelties within *Homo erectus*) and extrinsic factors (climatic and/or environmental changes) (Petraglia 2003, Anton & Swisher 2004, Lahr 2010, Agusti & Lordkipanidze 2011, Carotenuto *et al.* 2016). Although the environment in which these hominins lived must have played a role, there is currently no agreement whether early dispersal was more driven by intrinsic or extrinsic factors (Carotenuto *et al.* 2016).

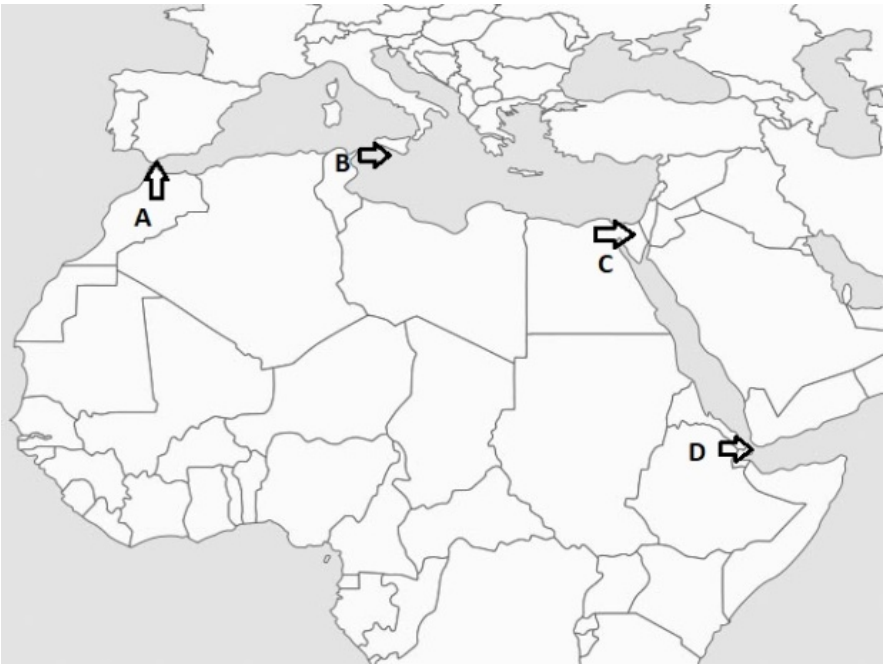


Figure 3.2: Potential points of entry from Africa into Eurasia. A: Gibraltar strait, B: Sicilian Channel, C: Sinaï Peninsula, D: Bab-El-Mandab Isthmus.

Theories emphasizing extrinsic factors in "Out of Africa I" generally assume that another condition, besides a physical connection between the source area and the destination area, may have needed to be fulfilled before *Homo erectus* dispersal could take place: the presence of suitable habitat. According to Vrba's (1995a) "Traffic Light model", climatic and environmental conditions in the connecting corridor and the destination area must first be optimal for a species, before it can expand (Vrba 1995a, Curran 2009). It is implied in this model that species dispersal is always part of a larger expansion of ecosystems and that animals will be restricted to regions with habitats of a similar nature to that in which they originally evolved (Curran 2009). Related to the "Traffic Light model", is Vrba's (1995a) "Turnover Pulse Theory" that goes even further and states that almost all major evolutionary trends such as speciation, dispersal and extinction are instigated by climatic and environmental change (Vrba 1995a). This model predicts that, in general, periods of radical climate change coincide with multiple extinction- and speciation events for different

mammalian lineages at the same time (Vrba 1995a). While there are indications in the fossil record that this is the case for certain groups such as the bovids (Vrba 1995a), the question remains whether the evolution and success of *Homo erectus* was also driven by such a climatic 'pulse' and its related environmental changes (Foley 1994).

If "Out of Africa I" was primarily instigated by such a climatic and environmental shift, evidence for this might be found in the form of palaeoclimatological and palaeoecological data indicating changes around the time *Homo erectus* started dispersing. Furthermore, if the first dispersal of *Homo* was part of a broader mammalian turnover, changes in the faunal composition as a result of (new) taxa appearing and/or disappearing at hominin localities might provide clues (Leakey & Werdelin 2010). Nevertheless, evidence from the carnivore, bovid and cercopithecid fossil records so far seems to suggest that there were no major dispersal events across multiple mammalian lineages at the time of Out of Africa I (Leakey & Werdelin 2010, O'Regan *et al.* 2011). Species that did expand their range during this period seem to have done so as a result of factors different from those that drove *Homo erectus* (Leakey & Werdelin 2010).

Palaeoecological and palaeoclimatological evidence, on the other hand, suggests that major environmental changes did take place broadly around the time that *Homo erectus* left East Africa. By most accounts, the Late Pliocene and Early Pleistocene were characterized by a shift to more open, arid environments with increasing seasonality (Bonnefille 1984, Prentice & Denton 1988, Demenocal 1995, Vrba 1996). According to multiple lines of evidence (e.g. palynological, isotopic, palaeozoological) this would have resulted in an expansion of open grasslands in East Africa with a substantial increase around 1.7 Ma (Bonnefille 1984, Cerling 1992, Demenocal 1995, Turner & Anton 2004, Curran 2009). Although the magnitude and timing of these environmental changes are not well understood (see e.g. Cerling 1992, Hertler *et al.* 2013), according to some researchers (Vrba 1996, Dennell & Roebroeks 2005, Dennell

2010) the spread of this type of grasslands wasn't restricted to East Africa, but was part of a wider expansion of a savannah-like environment across large stretches of Africa and Eurasia. The so called "Savannahstan model" advocates the existence of a connecting corridor of relatively uniform savannah environment that ranged from East Africa, over North Africa, the Middle East and Central Asia to East Asia (Fig. 3.3) (Dennell 2010). The authors argued that within this savannah belt the first members of *Homo* could actually have first evolved in Asia and from there spread to Africa instead of the other way around (Dennell & Roebroeks 2005, Dennell 2010). Although this thesis *a priori* assumes an 'Out of Africa' scenario for the origin of the genus *Homo*, the idea that the development and spread of a savannah belt was instrumental in the initial dispersal of our genus is tantalizing.

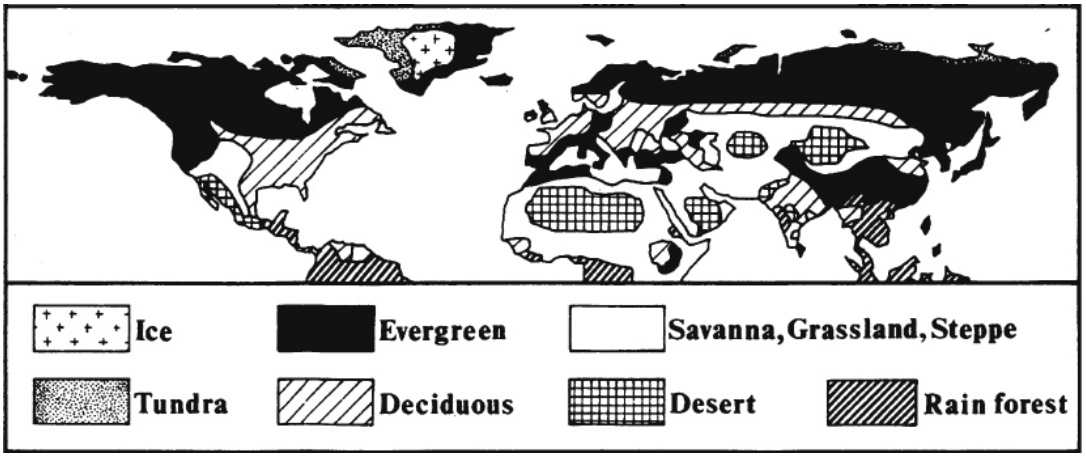


Figure 3.3: Purported distribution of savannah-like environments (white) during the Late Pliocene (adapted from Dowsett et al. 1994 in Dennell 2010)

On a regional level the idea of a continuous savannah belt has taken form in the "savannah corridor theory" in Southeast Asia (Heaney 1991, Bird *et al.* 2005). This theory arises from the idea that most mammal (including hominin) colonization of Java happened during glacial phases associated with low sea levels, exposing the Sunda shelf and connecting the principal islands to the mainland (de Vos *et al.* 1994, van den Bergh *et al.* 2001). Proponents of this

concept (Heaney 1991, Bird *et al.* 2005) have argued that the Southeast Asian palaeoenvironmental record suggests the presence of a connected tract of open vegetation from the Asian mainland to Java at several times during the (Early) Pleistocene. The rainforests currently predominant in Sundaland would only have gradually appeared over the course of the Pleistocene, but open environments would have re-colonized large tracts during glacial episodes. The resulting savannah corridor would have allowed for the spread of open-adapted species such as *Homo erectus* (Bird *et al.* 2005). Although the "Savannah corridor theory" was suggested to have been applicable to the Early Pleistocene, its main focus was actually on the presence of a dry corridor during the Last Glacial Maximum (Heaney 1991, Bird *et al*. 2005). The presence of such a savannah belt during the LGM has been contested and some (e.g. Meijaard 2003b, Stimpson 2010) have concluded that even during glacial maxima, forested environments persisted. As our knowledge of the palaeoenvironmental conditions during the earlier phases of the Pleistocene in this region is even more incomplete, evidence for the presence of a savannah corridor in the Early/Middle Pleistocene is limited.

Where the "Savannahstan model" and the "Savannah corridor theory" mainly stress the importance of savannah-like environments in the context of early *Homo* dispersal (Bird *et al.* 2005, Dennell & Roebroeks 2005, Dennell 2010), others have argued that a different type of environment was important for early expansion of *Homo erectus*. A number of authors have suggested that coastal zones and wetlands played a crucial role in this episode in human history (Stringer 2000, Joordens *et al*. 2009, Cohen *et al.* 2012). Hominin remains are often found in association with marine or lacustrine fauna (Joordens *et al.*2009) and many palaeoanthropological sites have an aquatic component in their proximity (Stringer 2000, Cohen *et al.* 2012). It was initially assumed that a focus on aquatic resources was a behavioural adaptation that didn't appear in hominins before the Late Palaeolithic (see Stiner 1994 and references therein), but more recently evidence has surfaced that such behaviour

could be much older and that early humans could have "coasted" their way out of Africa (Stringer 2000). Even though such explanations are mainly offered in the context of modern human expansion, some (Cohen *et al.* 2012) consider it likely that coastal zones provided important corridors for dispersal in earlier hominins as well.

Besides these theories that highlight the importance of specific environmental conditions in facilitating (or constraining) the dispersal of hominins, other theories place more emphasis on intrinsic changes in *Homo erectus* (Anton & Swisher 2004, Carotenuto *et al*. 2016). Important here is Potts' (1998) variability selection hypothesis. While this hypothesis does not necessarily contradict the trend towards more arid, open environments during the Plio-Pleistocene, it argues that an increase in climatic *fluctuations* from the Pliocene onward was a more important driver for hominin dispersal (Potts 1998, Bobe & Behrensmeyer 2004). It differs from theories that stress the selective effects associated with specific habitats and rather proposes that *Homo erectus* adapted to the quick and unpredictable climatic and environmental changes themselves that were typical for the Pleistocene (Potts 1998).

Such an increase in climatic oscillation is indeed seen in isotopic records from deep sea cores, especially from about 2.8 Ma (Prentice & Denton 1988) and was apparently paralleled by rapidly changing environmental conditions. This is for example evidenced in the palynological record in Europe, where glacial and interglacial cycles were mirrored by contractions and expansions of temperate deciduous forest-habitats and cold dry steppe environments (Potts 1998, Van Kolfschoten *et al.* 2015). More evidence comes from sedimentological records in North Africa, where numerous rich organic layers are found interspersed with sterile strata, clearly in association with glacial/interglacial cycles (Jenkins & Williams 1984, Potts 1998). In such a continuously changing world it might have been more advantageous for hominins to adapt to environmental change *itself* than to a specific type of environment (Potts 1998).

Which adaptations could have led to the success of early *Homo* when confronted with such inconsistent selection regimes (Potts 1998) is unclear. According to Potts (1998) there are nevertheless a number of anatomical and/or behavioural features in hominins that would qualify as variability selection adaptations. One such adaptation is bipedality. Although already developed by earlier homimins (*Australopithecus*), this adaptation would allow for locomotor versatility, suitable for both open- and arboreal environments (Potts 1998). The postcranial morphology of *Homo erectus* is more similar to that of modern humans than that of the australopithecines (Collard & Wood 2015), which could perhaps signify a further development in locomotor versatility.

Another adaptation that could perhaps have played an important role was the development of stone tools. This technology would have allowed access to food -such as bone marrow, meat or deeply buried tubers- that was previously unavailable and thus permitted more dietary flexibility (Potts 1998). Stone tools have been in use since at least the advent of the first members of the genus *Homo* (Harris 1983a), but *Homo erectus* probably was the first species to develop the more advanced Acheulean technology (Haviland *et al.* 2013). Although the first dispersal of *Homo erectus* may have antedated the appearance of the Acheulean (Anton & Swisher 2004), there is little doubt that the use of stone tools allowed hominins to exploit a wider range of resources. Especially in drier, open habitats where edible plants are harder to procure, the use of lithic technology may have allowed hominins to acquire meat on a more regular basis (Shipman & Walker 1989). Whether or not the shift towards increased carnivory in hominins was directly related to the development of (a specific) lithic technology, it is likely that it first appeared in *Homo erectus* (Shipman & Walker 1989, Carotenuto *et al.* 2016). In fact it is argued that hominins at this stage changed from occupying a primarily omnivorous niche to becoming top predators (Turner 1999, Carotenuto *et al.* 2016).

A third adaptation, that is perhaps related to a more carnivorous diet (Aiello & Wheeler 1995, Ferarro *et al.* 2013) and that may have resulted from variability selection, is the trend towards increasing encephalization in hominins (Potts 1998). The human adaptive niche is strongly shaped around social and technological complexities and the increase in brain size in the last two million years must have profoundly affected economic and social organization (Hublin *et al*. 2015). It is known that in primates there is a correlation between neocortex size and social group size, suggesting bigger brains allow for more advanced ecological problem solving (Jerison 1973) and the development of complex social interactions needed in large groups (Adolphs 1999, Dunbar 2003). Such larger groups could have functioned as information sharing units, having several ecological advantages such as pooling the (technological) innovations of group members, avoidance of trial-and-error learning (e.g. eating poisonous plants) and sharing of information about rare ecological events (e.g. a drought only experienced by the oldest group members) (Mithen 1994). Such an enhanced behavioural flexibility must certainly have increased ecological flexibility (Potts 1998). The advantages of increased social cooperation are moreover exemplified in extant human foraging societies who have as a result of intense social cooperation and food sharing, a higher rate of energy extraction from their environment than the smaller brained extant apes (Kaplan *et al.* 2000). As *Homo erectus* underwent a major shift in encephalization (Wood & Collard 1999) this factor could potentially have contributed to its success as a species and to its dispersal.

Nevertheless, even if we assume that the dispersal of *Homo erectus* was primarily instigated by intrinsic changes in morphology and behaviour resulting from variability selection, it remains hard to verify which adaptations were crucial to its success. What can be more easily tested, is whether *Homo erectus* was indeed able to thrive in a multitude of environments after its expansion from Africa or if the species was restricted to a specific type of environment. Perhaps the success and dispersal of *Homo erectus* can only be explained as the result of an

expansion of the habitats it originally evolved in? This is in essence also a question about the modernity of *Homo sapiens* behaviour. Is the capacity to adapt to a broad range of environments, as seen in modern humans (Potts 1998), a more recent phenomenon unique to our own species, or did earlier members of our genus already develop a similar flexibility?

3.5.4 Concluding remarks

Although palaeoenvironmental data is available from a number of *Homo erectus* sites in Africa and Eurasia, there are large discrepancies in our knowledge between regions and individual sites. Moreover, a high number of different approaches and proxies have been used to reconstruct ancient environmental conditions. Consequently, the results cannot always be easily compared and at times different methods have resulted in conflicting interpretations. Nevertheless, some patterns seem to emerge. It appears that for most African *Homo erectus* sites, palaeoenvironmental conditions have been interpreted as relatively dry and open. Especially in East Africa there is substantial evidence for an aridification of the landscape around the time *Homo erectus* appeared. This would be in line with an extrinsic explanation for early hominin dispersal such as the Savannahstan model (Dennell & Roebroeks 2005, Dennell 2010). Further afield there is also limited evidence that this trend towards drier, more open environments took place in South Africa, parts of Asia and North Africa. The exact timing and magnitude of these changes is poorly understood. There may be indications that these environmental changes already set in earlier and it is unclear how instrumental they were in driving hominin dispersal. In the light of these observations, it is interesting to note that a number of sites, especially in Asia, do not seem to exactly follow the patterns described above. Sites such as Kobacas and certain levels of Sangiran have been described as humid, wetland sites. This could point towards an increased adaptive flexibility in *Homo erectus* as proposed in Pott's (1998) variability selection hypothesis. Finally, if the presence of open, dry landscape was not a necessary requirement for *Homo erectus*, we might ask ourselves the

question whether the presence of a wet component in the landscape was important. It should be taken into account that this could potentially be another extrinsic factor influencing hominin dispersal.

4. Cervids and ecomorphology

4.1 Ecomorphology

Ecomorphology is but one approach within the field of morphology (Bock 1994). According to Bock (1994) there are four primary approaches or aspects in vertebrate morphology: descriptive, functional, evolutionary and ecological. The descriptive aspect of morphology, as is implied in the name, describes the material composition and morphological attributes of a biological entity and defines the limits of the system of attributes in an individual. Descriptive morphology forms an important prerequisite for the further understanding of the other morphological aspects (Bock 1994).

The functional aspect describes morphological function as related to the full set of features arising from the form at all levels of organization (Bock & Von Walhert 1965, Bock 1994). Relying on the descriptive aspect, functional morphology attempts to establish correlations between properties of the form and the function of features (Bock 1994). Once established, these correlations can be used to explain functional properties of animals of known morphological form (Bock 1994). Evolutionary morphology covers a wide range of morphological studies and often includes descriptive and functional aspects, but different from the other aspects (ecological, functional and descriptive), it offers a historical-narrative explanation (Bock 1991, 1994).

Ecomorphology can in the broadest sense be described as the discipline that "occupies itself with the connection between the shape of the animal in its entirety and its surroundings" (Van der Klaauw 1948, p. 27). It is concerned with the adaptiveness of morphological features and their correlation with the function of features. As such it is dependent on the results of functional morphological studies but places the emphasis on the biological or ecological role of the organism and not on the function itself (Bock 1994). Furthermore, *within* ecomorphology there are two different principal approaches. The first one's aim is to

determine adaptiveness of morphological features or systems within individual species, followed by comparison of these adaptations in different species, closely related or not (Bock 1994). In a second approach, more relevant to this dissertation, the emphasis is more ecological and studies the adaptive features within a group of (usually closely related) species and tries to determine the composition of communities, niche structure and other ecological parameters (Bock 1994). It essentially deals with the covariation between ecology and morphology but draws strongly on the descriptive and functional aspects (Winkler 1988, Bock 1994).

For this dissertation it will further suffice to say that Bock (1994) is followed and that a distinction is made between functional morphology, dealing with correlations between properties of the form and the function of features, and ecological morphology, the study of functional aspects of organisms and attributes in relationship to their environment (Bock 1994). In this sense it is similar to the definitions for ecomorphology used in many other palaeoecologically oriented studies (e.g. Kappelman 1988, Bishop 1994, Weinand 2005, Kovarovic & Andrews 2007). I do not follow Degusta and Vrba (2003) in their use of the term functional morphology, which includes ecological aspects.

4.2 Artiodactyl ecomorphology in palaeoanthropology

Mammalian ecomorphology draws its theoretical basis from the observation that species occupying comparable habitats display similar, convergent, adaptations (Andrews & Hixon 2014). This is expressed in phylogenetically unrelated taxa developing similar adaptive features as a result of being subjected to the same selective pressures (Andrews & Hixon 2014). While in biological anthropology this principle has been directly applied on human and non-human primate osteological elements with the goal of inferring correlations between morphological and ecological aspects in those species (e.g. Stern & Susman 1983, Cardini *et al.* 2007, Ungar 2011, Green & Alemseged 2012, Elton *et al*. 2016), more important in this

discussion is the use of ecomorphology on non-primate fossils, to be used as proxies for reconstructing hominin palaeoenvironments. Ecomorphological studies of this kind have been applied on a number of mammalian groups, such as canids (Meloro & Louys 2011), felids (Meloro *et al.* 2013), ursids (Figuerido *et al.* 2009), bats (Stimpson 2010), rodents (Fernandez & Campomanes 2003), equids (Scott 2004, Schellhorn 2009, Schellhorn & Pfretzschner 2015) and suids (Bishop 1994, Bishop *et al*. 2006, Cuddahee 2008), but the family on which this methodology has been used most commonly is that of the Bovidae. This is especially true for studies that have focused on the (ecological) morphology of the locomotor system (e.g. Kappelman 1988, Kappelman *et al.* 1997, Vrba 1980, 1995b, 1999, Plummer & Bishop 1994, Degusta & Vrba 2003, 2005a, 2005b, Scott 2004, Weinand 2005, Kovarovic & Andrews 2007, Plummer *et al*. 2008, Schellhorn 2009, Klein *et al*. 2010, Barr 2014a, 2017). Given the wealth of research that has been conducted on this family and because of its taxonomic relatedness to the Cervidae (Geist 1998, Janis 2007), our review on artiodactyl ecomorphology will have a strong focus on this family. The validity of the assumption that cervids are in many ways comparable to bovids when used in an ecomorphological study, will be further explored in section 4.5.

The functional morphology of the limb bones in bovids has long been established to be strongly influenced by environmental conditions (Gentry 1970, Oboussier & Ernst 1979, Leinders 1979, Scott 1983, 1985, 1987). More traditional palaeoenvironmental reconstructions based on bovid remains have heavily focused on the presence or absence of certain taxa in the fossil record (e.g. Vrba 1975, Gentry & Gentry 1978, Shipman and Harris 1988). This method has the weakness that it relies on taxonomic uniformitarianism, assuming that extinct species had ecological preferences similar to those of their closest living relatives (Andrews 1995), an assumption not necessarily valid (Dodd & Stanton 1990).

Ecomorphology on the other hand is often called a taxon-free method (Kovarovic & Andrews 2007, Andrews & Hixon 2014) and has the advantage that it can be applied on fossil remains that have not been identified beyond the family level (see Klein *et al*. 2010). In other words, ecological morphology can provide a more direct reconstruction of past habitats, as it asks 'how' an animal moved through a habitat instead of 'who' is present in the fossil record (Curran 2009).

Working within this framework, the last decades have seen a number of researchers developing bovid ecomorphological models that are palaeoecologically informative (e.g. Vrba 1980, 1995b, 1999, Köhler 1993, Kappelman 1988, Kappelman *et al.* 1997, Plummer & Bishop 1994, Degusta & Vrba 2003, 2005a, 2005b, Scott 2004, Weinand 2005, Kovarovic & Andrews 2007, Plummer *et al*. 2008, Klein *et al*. 2010, Barr 2014a, Barr 2018). The best studied aspects in bovid ecomorphology are probably the shape of the femur, astragalus and metapodials (e.g. Kappelman 1988, Kappelman *et al.* 1997, Plummer & Bishop 1994, Degusta & Vrba 2003, Kovarovic 2004, Scott 2004, Weinand 2005, Schellhorn 2009). Moreover these elements illustrate well how ecomorphology can be used on artiodactyls elements in palaeoanthropological contexts.

An early example for the metapodials is the work by Kathleen Scott (1983, 1985, 1987), who found that the metacarpus and metatarsus, as well as some other distal limb bones, varied with habitat. Species living in more open habitats typically had relatively longer metapodials, while species found in more closed environments had shorter metapodials (Scott 1985). Although Scott (1983, 1985, 1987) didn't explicitly dwell on the functional aspects that lie at the basis of this ecomorphological correlation, her observations were picked up by others (e.g. Plummer & Bishop 1994, Scott 2004, Klein *et al.* 2010) who realized its potential for habitat reconstructions and related it functionally to differences in joint stabilization and lever arm length. Studies of the femur have been particularly important in bovid ecomorphology. Gentry

(1970) was the first to establish that femoral morphology is closely related to locomotor behaviour and environment, but especially Kappelman's (1988) study has been influential. Kappelman (1988) argued that variation in the shape of the caput femoris is linked to differences in locomotor behaviour between species that are adapted to open environments (e.g. savannah) and species adapted to closed environments (e.g. forest). Bovids with more 'rectangularly' shaped femoral heads are found in open habitats while bovids with 'spherically' shaped femoral heads are found in more closed environments (Fig. 4.1). As there are few obstacles to evade in open landscapes when escaping predators, bovids living in such environments optimize cursorial efficiency by limiting axial rotation and abduction in the hip joint (Kappelman 1988). Bovids adapted to closed environments allow more axial rotation and abduction in the hip-joint for better maneuverability in dense vegetation (Kappelman 1988). Animals being pursued through dense vegetation tend to place obstacles between themselves and a pursuing predator (Curran 2009). It is worth mentioning that such differences in femoral head shape have also evolved between cursorial and saltatorial carnivores (Jenkins & Camazine 1977, Kappelman 1988).

The astragalus, having been studied by several researchers (Degusta & Vrba 2003, Kovarovic 2004, Kovarovic & Andrews 2007, Weinand 2005, 2007, Plummer *et al*. 2008, Schellhorn 2009, Barr 2014a), has proven to be a useful element in ecomorphology, as well. Similar to the femur, functional differences in the astragalus have been explained as the results of differences between a more cursorial or saltatorial locomotor strategy. Animals adapted to open environments tend to have relatively shorter astragali as they increase the range of angular excursion in the hock joint (Barr 2014a). Cursorial bovids adapted to open environments are also thought to have a larger trochlear articular surface, as a means to dissipate increased loads during fast running (Barr 2014a).

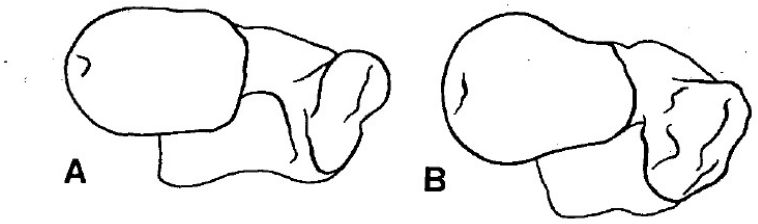


Figure 4.1: Proximal articulation of bovid femurs typical of environments with open vegetation (A) and closed vegetation (B) (adapted after Kappelman 1988).

Although a number of other correlations between morphological traits and ecological variables have been described in the literature on artiodactyl ecomorphology (see e.g. Degusta & Vrba 2005a, 2005b, Kovarovic & Andrews 2007, Schellhorn 2009), research into the biomechanics and underlying functional explanations of the bovid limb has generally received less attention (Vrba 1980, Curran 2009). Most researchers (Jenkins and Camazine 1977, Leinders 1979, Kappelman 1988, Scott 2004, Barr 2014a) agree that predator avoidance is the principle constraint on bovid locomotor morphology and that variation in limb morphology is driven by differences in vegetation and/or substrate type, each associated with unique escape strategies (Kappelman 1988, Leinders 1979, Köhler 1993). How these morphological traits are biomechanically linked with ecological parameters has been comparatively neglected. Some ecomorphologists (Degusta & Vrba 2003, 2005a) have even explicitly abstained from providing functional explanations, as they felt it was safer to wait for more rigorous biomechanical analyses than to provide "speculative" hypotheses. Others (Curran 2009, Barr 2014a, 2014b, Scott & Barr 2014a) have advocated that even though a more detailed understanding of functional morphology and its relationship to locomotion would be useful, it shouldn't keep us from developing interpretations based on observations and on what is known from the available literature.

In ideal circumstances ecomorphological hypotheses and their functional bases are tested experimentally on living specimens (Wainwright 1994). This is unfortunately impractical on large animals such as bovids, but a substantial body of literature is available (e.g. Leinders 1979, Köhler 1993, Curran 2009, 2012, Scott 2004, Scott & Barr 2014, Barr 2014a, Barr 2018) that provides useful discussions about the underlying biomechanical aspects that are at the basis of morphological variation in artiodactyl limb bones. It is therefore the intention in this dissertation to provide a theoretical framework based on the literature and on direct observations of limb bone anatomy, as a foundation in functional morphology on which further ecomorphological correlations can be based.

Ecomorphological studies are usually conducted in a typical way by combining data from behavioural ecology with osteomorphometric data of extant and ultimately fossil specimens (e.g. Plummer & Bishop 1994, Degusta & Vrba 2003, 2005a, Scott 2004, Weinand 2005, Kovarovic & Andrews 2007, Plummer *et al*. 2008). Typically, a model is first constructed, based on data from extant species of known taxonomy and habitat preference. To avoid overcomplicating the model, habitat preferences are almost always summarized into a limited number of broad habitat categories such as "closed vegetation" or "open vegetation" (Kappelman *et al*. 1997, Curran 2009). In most studies (e.g. Plummer & Bishop 1994, Weinand 2005, Kovarovic & Andrews 2007), the morphology of the limb bones is quantified by taking measurements on the bones, although in some cases non metric traits are used as well (e.g. Degusta & Vrba 2005b). When a morphometric approach is used, data is usually gathered by collecting linear measurements from key landmarks on the skeleton (e.g. Kappelman 1988, Degusta & Vrba 2003, 2005a, Kovarovic & Andrews 2007). The resulting variables in that case are often standardized for body size before meaningful comparisons can be made (Curran 2009), but some recent studies (Curran 2009, 2012, Borphy *et al*. 2014) have made use of geometric morphometrics, an alternative approach that by-passes the need to

control for (isometric) body size differences. Regardless of which method is used, morphometric data will invariably result in high numbers of variables that can be analyzed using a range of multivariate statistical tests. These are often dimensionality reduction techniques, producing linear recombinations of original variables by maximizing variability in the dataset (Mendoza *et al*. 2002). Techniques typically used are Principal Component Analysis (PCA) (e.g. Curran 2009), Discriminant Function Analysis (DFA) (e.g. Kovarovic & Andrews 2007), and Factor Analysis (FA) (e.g. Schellhorn & Pfretzschner 2015). By means of these statistical analyses an estimate can be made of how well morphological variation correlates with differences in habitat (Curran 2009). In a second phase the same measurements, this time taken on fossil specimens, are added to the dataset. By assessing the behaviour of the fossil specimens in a dataset relative to the data collected on extant specimens, predictions can be made about the ecology of extinct taxa.

So far most artiodactyl ecomorphological research has focused on reconstructing African palaeoenvironments ((e.g. Vrba 1980, 1995b, 1999, Kappelman 1988, Kappelman *et al.* 1997, Bishop 1994, Plummer & Bishop 1994, Degusta & Vrba 2003, 2005a, 2005b, Scott 2004, Kovarovic & Andrews 2007, Plummer *et al*. 2008, Klein *et al*. 2010, Barr 2014a, 2014b, 2015, 2017). Only a limited number of studies have focused on the palaeoecology of Eurasian assemblages. Some notable exceptions are Curran (2009, 2012) who worked on cervid fossils from the Pleistocene of Europe and the Middle East and Scott (2004) who reconstructed palaeoenvironments of Miocene hominoid sites in Europe and Asia based on equid and bovid remains. Weinand (2005, 2007) developed a model for the bovid astragalus and applied it on fossil assemblages from two Pleistocene sites from Java, that also form an important part of this dissertation (Kedung Brubus and Trinil). In addition, Arif and de Vos (2011) applied Kappelman's (1988) method in a pilot study on some bovid femurs from Trinil.

4.3 Problems and limitations

Although ecomorphology has the advantage that it makes use of easily quantified data (Andrews & Hixon 2014) and that it does not rely as much on taxonomic unformitarianism as methods based on species diversity (Andrews 1995), it also poses some problems in itself. One question that could be asked about ecomorphology, is how independent of taxonomy this method really is. Although ecomorphology is often dubbed a "taxon-free" method because it does not require specific identifications of fossil specimens (Barr 2014a), there are reasons to assume this is only partially true. An issue that was recently raised in this context is that individual datapoints in an ecomorphological training set of extant species cannot be considered independent, as they are related to one another in a hierarchical phylogeny (Klein *et al*. 2010, Barr 2014a). Closely related species, having common ancestors, often share morphological and ecological characteristics because they inherited them from their ancestors and not always because they are adapted to similar environments (Barr 2014a). This is illustrated by a study of Klein and colleagues (2010) who realized that in their analysis of bovid metapodials a number of species of the same habitat plotted out differently along the axes of their PCA. According to the authors this was to a large extent due to morphological similarities and differences that resulted from phylogenetic relatedness rather than from purely functional differences (Klein *et al.* 2010, Scott & Barr 2014). The problem is further complicated by the fact that habitat preference itself may to some extent be driven by phylogeny in certain mammalian families. It is for example known that a number of bovid lineages tend to specialize in particular habitats (Vrba 1980, Kappelman 1984, Shipman & Harris 1988, Barr 2014a, 2014b). As a result, many bovid species assigned to specific habitat categories will often also be closely related to each other (Barr 2014a). Ecomorphological models based on such species or families may give biased results if they are interpreted without taking this factor into account.

Partially in response to this critique a number of statistical methods and measures have been used –mainly phylogenetic comparative methods- that deal with the issue of phylogenetic non-independence (Meloro 2007, Meloro *et al.* 2008, Meloro & Louys 2011, Meloro *et al.* 2013, Barr 2014a, Barr & Scott 2014). Some well known methods that have been used in this context are phylogenetic independent contrasts, a method in which standardized contrasts are calculated that form the difference between trait values of species weighed by their evolutionary distance (Felsenstein 1985, Monteiro 2013) and the more recently proposed Phylogenetic Principal Components Analysis (PPCA), which works similar to a standard PCA, but where the ordination of multivariate data is phylogenetically weighed (Polly *et al.* 2013a). In (artiodactyl) osteological studies Phylogenetic Generalized Least Squares (PGLS) (Grafen 1989) has probably been the most commonly used method (e.g. Meloro 2007, 2008, Walmsley *et al.* 2012, Barr 2014a, 2014b, Curran 2015, Van Heteren *et al*. 2015). In this type of weighed regression phylogeny is incorporated as an error term during regression of shape variables on e.g. locomotor or ecological categories (Martins & Hansen 1997, Walmsley *et al.* 2012). As such, PGLS provides a flexible and formal statistical method to estimate the presence and magnitude of a phylogenetic signal in a given dataset (Barr 2014a).

A similar issue, also highlighted by Klein and colleagues (2010) is the presence of a second confounding factor complicating ecomorphological analyses: body size. In their study on bovid metapodials Klein et al. (2010) noted that besides phylogeny, size differences between species also had an important effect on statistical separations along the axes of their PCA. This problem of the influence of body size on the mammal skeleton has concerned other ecomorphologists before (e.g. Scott 2004, Curran 2009, Meloro *et al*. 2013, Van Heteren *et al.* 2015). It should nevertheless be mentioned that body size in itself can be considered an ecomorphological character (Andrews & Hixon 2014). As an animals' size is closely related to locomotion, energy requirements and dietary requirements, it can be correlated with certain

life history variables (Geist 1998). In artiodactyls this is, for example, illustrated by the Jarman-Bell principle (Bell 1970, Jarman 1974) that poses that small bodied species with high metabolic rates, but low energy requirements, generally prefer high quality food items that are more widely distributed. Large bodied species with low metabolic rates on the other hand often have to be less selective and focus on more commonly availably low quality grasses that contain higher amounts of fiber (Kovarovic 2004). In addition, body size also has an effect on predator evasion strategies and social organisation. Some smaller species might have a more solitary lifestyle and hide when pursued by predators. Other, larger forms often have a more gregarious lifestyle and rely on herds as an anti-predatory strategy (Jarman 1974, Geist 1998). Despite the established association between body size and ecology, the exact relationships between these factors are not well understood and within the context of individual mammalian families instead of entire communities, it is thought that body size is not a particularly good predictor for habitat preference (Kovarovic 2004). Hence there are arguments against including the effects of body size in ecomorphological studies. In families with substantial between-species size variation it is likely that body size will consistently account for the majority of morphometric differences in an ecomorphological dataset when not accounted for (Kovarovic 2004). As a result many ecomorphological studies have included size correcting procedures in their models. Some of these methods (e.g. Scott 2004) have simply attempted to reduce the effect of isometric size differences by making use of ratio's, other studies (e.g. Kovarovic 2004) used more complex (regression) techniques that control the effects of isometric as well as allometric differences.

Klein *et al*. (2010) were rather pessimistic about the confounding effects of phylogeny and body size in ecomorphological studies and suggested that many models based on postcranial elements merely capture phylogenetic and body size differences and much less functional differences related to habitat. Many others (e.g. Kappelman 1991, Kovarovic 2004, Barr

2014a, 2014b) have nevertheless clearly demonstrated that distantly related species living in the same habitats often display similar, convergent adaptations in their skeletal morphology. In this dissertation the latter authors are followed and it is believed that by providing a adequate functional framework to support potential ecomorphological correlations and by sufficiently accounting for confounding factors such as size and phylogeny, predictions *can* be made about habitat preferences of fossil taxa based on functional differences.

A final problem, of a different kind, is that the nature of ecomorphological studies and the way in which morphometric data is analysed, requires that species are assigned to a limited number of habitat categories (Curran 2009). On the one hand this has the problem that some species cannot be easily placed in one category, as they can perhaps be found in different habitats or because their ecology is less well known. More problematic is that the categories themselves are always an oversimplification of ecological reality as habitat variation is lost in single categories (Curran 2009). Although further breaking down the habitat continuum into a higher number of groups could potentially allow for more accurate palaeoenvironmental reconstructions, it reduces the ability of statistical models to correctly classify specimens in the right habitat category. Curran (2009) found that in bovid studies, models that applied higher numbers of habitat groups systematically had a lower success rate of reclassification. This dissertation will make use of five to six habitat categories as a consensus. Being on the high side, compared to some bovid studies (Kappelman 1988, Plummer & Bishop 1994, Degusta & Vrba 2003, Scott 2004) it attempts to minimize loss of habitat specificity while at the same time acknowledging that any of the current models are a compromise between operationality and resolution.

4.4 Extant and fossil cervids

4.4.1 Extant cervids

4.4.1.1 Origins and evolution

The cervidae, or colloquially deer, are a family in the order Artiodactyla, or even toed ungulates (Kingdon 1997). This order is currently the predominant ungulate order and includes 10 families, 85 genera and 217 species (Janis 2007). The artiodactyls appeared in the Eocene around 55 million years ago (Gentry 2000) and were probably related to a primitive group of herbivores called the condylarths (Rose 1996). While initially the artiodactyls only consisted of a few small forms of less than 5 kg, towards the Middle Eocene this group diversified into a large number of taxa and started to replace the previously dominant perissodactyls (Janis 2007). By the late Middle Eocene three suborders had appeared: Tylopoda, Suina and Ruminantia (Janis & Scott 1987). It was the suborder of the Ruminantia that ultimately became the most successful and to which today most artiodactyls belong. During the Miocene, the artiodactyl order reached its height in terms of diversity and many new forms appeared. Besides the Bovidae, a number of other families, such as the Giraffidae, Palaeomericydae, Antilocapridae and Camelidae diversified into a large number of species, many of which are now extinct (Janis 2007).

Although the phylogenetic history of cervids is still unresolved (di Stephano & Petronio 2002, Heckeberg *et al*. 2016, Heckeberg 2020), deer evolution should be considered as part of broader artiodactyl evolution (Geist 1998). This family likely evolved from the group of ruminants called the Palaeomerycidae, which also gave rise to the Giraffidae (Kurten 2007). While cervids have long been considered primitive members of the artiodactyl lineage, it has by now been demonstrated that they also possess a number of derived characters, such as a closed metatarsal gully (Leinders & Heintz 1980, Janis *et al.* 1998). Even though it is true that deer evolution started in the Miocene with small, primitive, slinker type animals, they soon

developed into a range of new forms (Geist 1998, Curran 2009). These early primitive deer were antlerless, of small stature and with large canines, not unlike today's muntjacs (Geist 1998). About 20 million years ago, the family radiated into a number of taxa, characterized by a larger size and more adapted to open landscapes (Clutton-Brock *et al*. 1982, Curran 2009).

Deer radiation appears to have happened in a number of phases that were influenced by changes in distribution and environment (Geist 1998). In a first radiation, small duiker like forms radiated from tropical forest environments into a number of open habitat forms. In a second phase, during the Middle Miocene, three prong antlered deer evolved and spread into more temperate zones (Curran 2009). The Plio-Pleistocene period marked a third radiation event and was the era when cervids reached their greatest diversity. It saw the appearance of four prong antlered deer in more northern, open areas (Geist 1998).

Until the Pliocene, deer were restricted to Eurasia, but probably increasing diversity and population pressure, as a result of climatic changes, led to cervids dispersing from Eurasia into new areas of the Old and New World (Heintz *et al*. 1990). India and Indonesia were probably colonized some 3 million years ago and North America about 5 million years ago (Heintz *et al*. 1990, Curran 2009). South America was colonized much later than North America. Before the Pliocene, the former continent had its own unique megafauna that had evolved in isolation from the North American continent. Around 3 to 3.5 million years ago, the uprising of the Panama Isthmus led to the connection of the two continental plates and resulted in an event called the 'great American biotic interchange', during which many species were exchanged between the North- and South America. This event included cervids spreading to South America and occupying a range of niches on this continent (Geist 1998).

Of the current cervid tribes, the Capreolini and Muntiacini probably originated in the Middle Miocene (Pitra *et al*. 2004, Groves 2007). The Cervini, Odocoileini and Alceini appeared in the Late-Miocene and Early-Pliocene (Gentry 2000). The extant deer genera originate in the

Plio-Pleistocene, with *Odocoileus* probably being the oldest genus with an age of more than 5 million years (Kurten & Anderson 1980, Geist 1998). Most extant species, such as roe deer (*Capreolus capreolus*), moose (*Alces alces*) or red deer (*Cervus elaphus*) have their origin in the Middle and Late Pleistocene (Kurten 2007).

Although cervids were part of a wider and increasing diversification in artiodactyls during the Late Tertiary and Quaternary, deer took their own unique evolutionary path, which led to a number of characteristics that set them apart from other families, such as the bovids and giraffids (Geist 1998, Janis 2007). Some conspicuous traits evolved by deer are antlers, a primitive, low crowned dentition (Kurten 2007), and a bovid like body plan (Kingdon 1997).

Cervids range in size between the diminutive pudu (*Pudu puda*), that weighs only 3.3 to 6 kg and the huge moose (*Alces alces*) that can weigh up to 600 kg (Geist 1998). Giant forms such as moose and Irish elk (*Megaloceros giganteus*) are typical taxa of the Pleistocene period and were able to develop because high quality food was seasonally abundant in colder environments (Geist 1998). These large species were mainly a phenomenon of the Old World and never evolved in the Americas, probably due to competition with the more specialized endemic megafauna (Curran 2009). After the Late Pleistocene megafaunal extinctions in North America, a number of newly opened niches were re-occupied by some of these giant Old World deer (Geist 1998). Smaller dwarf forms, such as the Bawean deer (*Axis kuhlii*), are often found on islands. This is a result of efficiency selection, whereby animals increase fitness if they are able to take resources for maintenance and use them for reproduction. The lack of predators in such isolated environments allows animals to invest more in reproduction (Geist 1998). Other cervids of small stature, such as the brockets (*Mazama* spp.) secondarily evolved into primitive looking, small species, as an adaptation to habitats with dense vegetation in South America (Geist 1998).

Deer in general retain a rather primitive, low crowned dentition in comparison with bovids (Kurten 2007). This is related to the fact that deer never evolved into true grazing specialists like many of the Bovidae (Janis 2007). Instead of competing with the latter family for harder fibered forage, deer evolved to be more opportunistic feeders, removing high quality, nutrient rich food wherever it is found (Geist 1998). As result deer are not as well adapted to open environments as bovids and few species are found in truly open habitats (Geist 1998).

A final important trait that evolved in many deer species is antlers. The only species that currently lacks them is the water deer (*Hydropotes inermis*) (Geist 1998). These bony extensions of the skull are usually only found in males, except in the reindeer (*Rangifer tarandus*). It first appeared in the genera *Dicrocerus* and *Stephanocemas* in the Middle-Miocene (Clutton-Brock *et al.* 1982). The antlers of these early members were small and covered with velvet, like in the giraffids (Geist 1998, Salmeron 2014), the closest living relatives of the cervids (Kurten 2007). In the Plio-Pleistocene antlers often reached impressive proportions. Antlers should be considered a luxury organ and a display of fitness (Geist 1998). They are shed on a regular basis and are used in fights between males for females (Whitaker *et al*. 1998). It is known that females often select the males with the largest antlers (Curran 2009).

4.4.1.2 Taxonomy

The taxonomy of cervids has been a topic of controversy for more than a century (di Stefano & Petronio 2002, Heckeberg *et al.* 2016). According to the classic taxonomic scheme by Groves & Grubb (1987) and a more recent concensus classification based on the literature (Heckeberg *et al.* 2016), there are two subfamilies of Cervidae: the Capreolinae and the Cervinae. The Capreolinae can be divived into four tribes: the Alceini, the Capreolini, the Odocoileini and the Rangiferini. The Cervinae on the other hand are composed of only two tribes: the Cervini and the Muntiacini. Of these six tribes only two occur in Southeast Asia:

the Cervini and the Muntiacini. The other tribes occur either in the more northern and western parts of Eurasia (Alceini, Capreolini and Rangiferini) or in North- and South America (Odocoileini, Rangiferini and Alceini) (Heckeberg *et al.* 2016). A schematic overview of deer taxonomy above species level is given in Figure 4.2.

A tribe with an important presence in Southeast Asia and which forms the main emphasis of this dissertation is that of the Cervini. In the taxonomic scheme by Groves and Grubb (1987) four genera are recognized in this group, with eight subgenera. The genus *Cervus* (sensu lato) is divided into four subgenera, namely *Rusa* (including *Cervus timorensis, Cervus unicolor, Cervus alfredi and Cervus mariannus*), *Rucervus* (containing *Cervus eldii, Cervus duvaucelli and Cervus schomburgki*), *Prezwalskium* (only *Cervus albirostris*) and *Cervus* (sensu stricto) (*Cervus elaphus* and *Cervus nippon*).

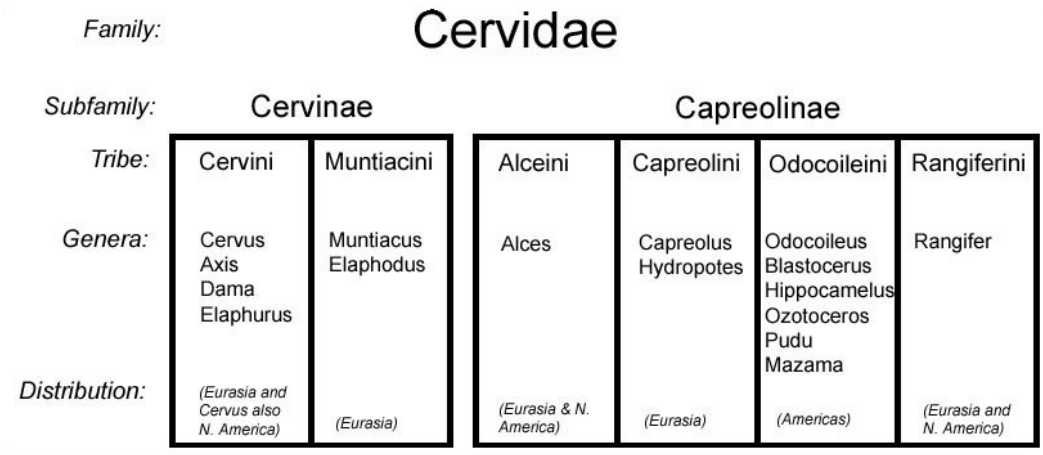


Figure 4.2: Overview of deer taxonomy above species level (adapted from Heckeberg et al. 2016).

A second genus in the tribe of the Cervini is *Axis*, composed of the subgenera *Axis* (containing only *Axis axis*) and *Hyelaphus* (containing *Axis kuhlii, Axis porcinus* and *Axis calamianensis*). The genus *Dama* is represented by *Dama dama* and the genus *Elaphurus* includes only Père

David's deer (*Elaphurus davidianus*), but may have been the result of hybridization between two unknown species (Groves & Grubb 1987), most likely of the *Rucervus* and *Cervus* subgenera (Meijaard & Groves 2004).

Recent genetic research has shed doubt on some of these relationships. Randi *et al.* (1998) argued for a fusion of the subgenera *Rucervus* and *Elaphurus*, based on mitochondrial DNA sequencing. In addition, they highlight the need for a revision of the subgenus *Rusa* (Randi *et al*. 1998). A mitochondrial DNA analysis by Pitra and colleagues (2004) proposed a number of changes on the generic level as well as the species level. According to their analyses, the Middle Eastern subspecies of *Dama dama*, should be awarded true species status as *Dama mesopotamica*. The subgenus *Hyelaphus* should be excluded from the genus *Axis* and considered its own genus, possibly more closely related to the *Rusa*-deer. *Elaphurus davidianus* is confirmed to belong to a genus separate from *Cervus* (s.l). All other species are placed under the genus *Cervus* (s.l.) with the exception of *Cervus eldii*, which is placed under its own genus (*Panolia*). The North American elk (*Cervus canadensis*) is separated from the European red deer (*Cervus elaphus*) and given species status (Pitra *et al*. 2004). As no definite consensus taxonomy is available for the Cervini at this point, I chose to maintain a relatively conservative view regarding this group based on the scheme by Groves and Grubb (1987), but keeping in mind more recent developments. A summary of the taxonomic scheme adhered to in this dissertation is given in Table 4.1.

The Muntiacini are a relatively diverse tribe that is also well represented in Southeast Asia (Groves & Grubb 2011). It is composed of two genera: *Muntiacus* and *Elaphodus*. The latter genus is monotypic and contains only *Elaphodus cephalopus* (Groves & Grubb 1987, 2011, Heckeberg 2016), *Muntiacus* is more diverse and traditionally most researchers distinguish five different species, as well as a number of subspecies (Groves 1982, Groves & Grubb 1987, Ma *et al*. 1986). Although a number of new species have been proposed in the last two

decades, such as *Muntiacus vuquangensis* and *Muntiacus putaoensis* (Groves 2011), I will adhere to the traditional scheme and recognize the following species: *Muntiacus muntjak, Muntiacus reevesi, Muntiacus rooseveltorum, Muntiacus feae* and *Muntiacus crinifrons*.

Genus	Subgenus	Species
Axis	*Axis*	Chital (*Axis axis*)
	Hyelaphus	Hog deer (*Axis porcinus*)
		Bawean deer (*Axis kuhlii*)
		Calamian deer (*Axis calamianensis*)
Dama	*Dama*	Fallow deer (*Dama dama*)
Cervus (s.l.)	*Cervus* (s.s.)	Red deer (*Cervus elaphus*)
		Sika deer (Cervus nippon)
	Przewalskium	White lipped deer (*Cervus albirostris*)
	Rucervus	Eld's deer (*Cervus eldii*)
		Barasingha (*Cervus duvaucelii*)
		Schomburgk's deer (*Cervus schomburgki*)
	Rusa	Sambar (*Cervus unicolor*)
		Javan rusa (*Cervus timorensis*)
		Philippine spotted deer (*Cervus alfredi*)
		Philippine deer (*Cervus mariannus*)
Elaphurus	*Elaphurus*	Pere David's deer (*Elaphurus davidianus*)

Table 4.1: Taxonomic scheme of the Cervini tribe (based on Groves &Grubb 1987)

The Odocoileini represent a controversial tribe of cervids, and systematic relationships in this clade are unresolved (Heckeberg *et al.* 2016). It consists of six genera: *Odocoileus, Mazama, Blastocerus, Hippocamelus, Pudu,* and *Ozotocerus*, of which the latter five are all placed in the subtribe Blastocerina and the genus *Odocoileus* in the subtribe Odocoileina (Heckeberg *et al.* 2016). The members of the Blastocerina subtribe are endemic to South America and are a clear example of adaptive radiation on this continent (Curran 2009). The relationship between the different genera and species is problematic, but Groves and Grubb (1987) recognize a number of different taxa in their taxonomic scheme which is also followed in this dissertation. Two species are recognized in the genus *Hippocamelus*: *Hippocamelus bisulcus* and *Hippocamelus anitisensis*. The genera *Blastocerus* and *Ozotoceros* are thought to be monotypic and include respectively *Blatocerus dichotomus* and *Ozotocerus bezoarticus*

(Groves & Grubb 1987). In the South American brockets (genus *Mazama*) several species are accepted by Groves and Grubb (1987): *Mazama americana, Mazama temana, Mazama gouazoubira, Mazama permira, Mazama rufina, Mazama chunyi* and possibly *Mazama brincenii* and *Mazama nana* (Groves & Grubb 1987, Geist 1998). Of the small pudu (*Pudu*), there are probably only two species: *Pudu mephistopheles* and *Pudu puda* (Groves & Grubb 1987, Geist 1998). *Odocoileus*, the only genus of the subtribe Odocoileina includes *Odocoileus virginianus* and *Odocoileus hemionus* (Groves & Grubb 1987, Geist 1998).

The Rangiferini tribe certainly includes only one species (*Rangifer tarandus*) (Groves & Grubb 1987, 2011) while the same is probably true for the Alceini (*Alces alces*) (Groves & Grubb 1987, Geist 1998), although some sources separate the North American moose (*Alces americanus*) on the species level (Groves & Grubb 2011). The Capreolini tribe consists of two genera: *Capreolus* and *Hydropotes*. In *Capreolus*, two species are recognized: *Capreolus capreolus* and *Capreolus pygarus*. In the genus *Hydropotes* there is only one species: *Hydropotes inermis* (Groves & Grubb 1987).

4.4.1.3 Ecology

Deer are able to subsist in a wide range of habitats, which is to be suspected in a family with a very wide distribution (Putman & Flueck 2011). Cervid habitats range from closed tropical rainforest (e.g. *Muntiacus muntjak*) (Ekwal *et al.* 2012) to semi-arid open grassland (e.g. *Ozotoceros bezoarticus*) (Merino & Semenjuk 2011). Some species have an extremely broad geographical range (e.g. *Cervus unicolor*) (Francis 2008), while others are restricted to small islands (e.g. *Axis kuhlii*) (Geist 1998). They are mostly species of tropical to temperate regions, but some taxa are adapted to more extreme conditions like reindeer (*Rangifer tarandus*) that live in the arctic tundra (Baskin 1986). Generally speaking, deer are probably best adapted to young, poorly stocked ecosystems (Geist 1998).

These extreme habitat differences are reflected in substantial variation in a number of physiological traits (e.g. in metabolic rate, digestion, heat tolerance and water management) that allow species to survive in these conditions (Putman & Flueck 2011). In part due to their increased metabolic rate, reindeer are, for example, able to tolerate temperatures down to -50°C (Geist 1998, Putman & Flueck 2011). The influence of body size and ambient temperature on water management in deer species is another example. Temperate forms like red deer (*Cervus elaphus*) tend to have a higher water intake than tropical species like Javan rusa (*Cervus timorensis*) (Yape Kii & Dryden 2005).

Cervid habitats not only differ in vegetation and climate, but also in terms of substrate type (wet or dry) and altitude. Certain species, like Eld's deer (*Cervus eldii*) and Chinese water deer (*Hydropotes inermis*) are clearly adapted to wet environments (Tordoff *et al.* 2005, Zhang *et al.* 2006), while other species such as white-lipped deer (*Cervus albirostris*) are found at high altitudes (Leslie 2010). It should however be mentioned that no deer are truly adapted to mountainous terrain in the way that some bovids are (Geist 1998). White-lipped deer have a preference for plains at high altitude and even the huemul (*Hippocamelus bisulcus*), traditionally considered a mountain deer, has been shown to occur mainly on flat terrain (Flueck & Flueck 2017).

In general, deer are not as specialized in terms of food habits as some bovids. High quality food with low amounts of fiber is preferred and is shredded and moved quickly trough the alimentary tract (Geist 1998). Deer are ruminants, meaning they have complex stomachs where food is digested mainly by means of microbial fermentation. Characteristic for this type of digestion is the regular regurgitation of partially digested food for re-chewing (rumination) (Whitfield 1986). Despite their preference for low fibered, high quality food, there is still considerable variation in dietary composition between deer species. Some forms, such as the white lipped deer (*Cervus alibirostris*), are able to include a substantial amount of graze in

their diets, while others (e.g. *Alces alces*) are true browsers that live on leaves and young shoots (Geist 1998). Slinker type deer (e.g. *Muntiacus reevesi*) usually feed on soft, easily digestible plants such as buds, flowers and fruit (Geist 1998), while more cursorial forms (e.g. *Axis axis*) are often more inclined towards grazing (Schaller 1967). Reindeer (*Rangifer tarandus*) are exceptional again, as a large part of their diet consists of nutrient poor lichens (Nieminen & Heiskari 1988).

Social organization in deer also differs substantially between taxa and is found to be correlated with environmental factors. Some species, like the chital (*Axis axis*), are highly gregarious (Schaller 1967), while others, such as the hog deer (*Axis porcinus*) tend to be more solitary (Fernando 1984). Usually, increased sociality in deer is found in animals living in more open environments and vice versa (Geist 1998). Besides environmental aspects, discrepancies in social organization between deer are also subject to other factors such as seasonal variation and differences in age and sex (Geist 1998).

Anti-predator adaptations are powerful drivers in deer evolution and have a profound influence on cervid morphology and behaviour (Geist 1998). Because areas outside their home range may be poorer in resources or are defended by conspecifics, deer can't just leave when a predator enters the area. As a result cervids have a number of anti-predator strategies to overcome such encounters (Geist 1998). One such strategy is to avoid being detected, by for example minimizing movement or masking scent (Geist 1998). Another tactic, used by e.g. muntjacs is the release of puffs of scent, marking objects in the surrounding area, which confuses predators (Ralls 1974, Geist 1998). Some species such as the chital (*Axis axis*) are adapted to living in herds as an anti-predatory countermeasure (Schaller 1967).

Once detected, however, deer will flee. Depending on the habitat in which an encounter takes place, deer have evolved different strategies to escape from their predators. These differences can be mainly summarized as an evolution from saltatorial hiders using obstructed surfaces to

cursorial movement specialists (Geist 1998). Species living in thick vegetation make use of two tactics. Small forms, such as the muntjacs (*Muntiacus* spp.), attempt to maximize the distance between themselves and the predator in order to gain time to hide (Geist 1998). For this they use e.g. trail tunnels through vegetation. As the pursuing predator is usually too large to easily pass through these tunnels, it is either blocked or slowed down by this strategy, allowing the prey to find cover (Geist 1998). Larger species that cannot rely on these trail tunnels make use of another strategy. These forms rely heavily on saltation (jumping or leaping) as a means to place objects such as branches or rocks between them and their pursuer (Geist 1998).They may also use steep slopes and give conflicting signals about their direction to the predator (Barrette 1977, Geist 1998). This strategy confuses and disorients the predator and allows the prey to escape (Geist 1998)

Other species living in more open habitats, devoid of objects that can be placed in between the predator and the fleeing animal, have developed a cursorial escape strategy. Such species are characterized by high speed and increased endurance (Geist 1998). For example red deer (*Cervus elaphus*) are known to easily outrun dogs or horses when being being chased by hunters (Geist 1998). Some species do not really belong in any of these categories (saltatorial or cursorial) and have developed their own unique evasion strategies. One such animal is the moose (*Alces alces*) which makes optimal use of its large size and long legs to place obstacles between itself and predators. While the moose can easily “glide” over obstacles by just stepping or trotting over them, predators like wolves will quickly tire from having to jump over them (Geist 1998) (Fig. 4.3).

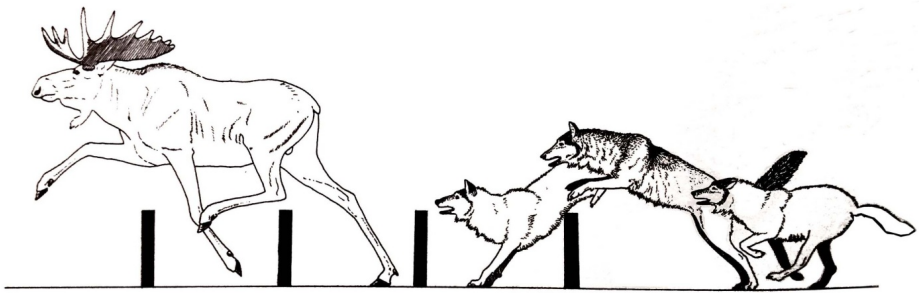


Figure 4.3: Moose escaping wolves by trotting over obstacles (adapted from Geist 1998)

Although there are strong indications for a general link between predator evasion strategies and habitat in cervids, there is little quantitative data available about how these evasion tactics translate into specific locomotor behaviours (Caro 1986, 1994). Knowledge of these specific locomotor behaviours is nevertheless important for the construction of ecomorphological models such as the ones in this dissertation. Fortunately, some research on bovids in African environments (Caro 1986, 1994, Caro *et al.* 2004) provides a good model that can most likely be extrapolated to the cervid family. Caron (1994) observed five different locomotor behaviours associated with predator evasion: leaping, bounding, prancing and tacking or zig-zag running. An overview with explanations is given in Table 4.2. In these studies it is pointed out that stotting and prancing probably act more as signals to wrongfoot the predator than as locomotor adaptations that directly help during flight (Caro 1994, 2004). Tacking, or zig-zag running, was found to be more common amongst bovids living in open habitats (Caro 2004) and bounding leaps were more likely to occur in bovids when the topography was more rugged or when vegetation was tall (Caro 1994). It is therefore likely that specific locomotor behaviours associated with saltatorial deer living in landscapes with closed vegetation are bounding and leaping, while cursorial deer, adapted to more open habitats probably emphasize tacking and increased speed when escaping pursuing predators.

Leap:	High jump where the individual rises vertically of the ground
Bound:	Long jump that carries the animal over at least double the distance covered by one galloping stride
Stot:	A bouncing gait with all four legs held stiff and straight, landing on all fours
Tack/zig-zag:	Sharp turn that suddenly changes course by approximately 90°
Prance:	Series of pronounced and exaggerated high steps made at slow speed, similar to the "piaffer gait" in race horses

Table 4.2: Locomotor behaviours associated with predator evasion (adapted after Caro 1994)

4.4.2 Quaternary cervids of Java and Sundaland

Fossil deer are known from a number of sites in Island Southeast Asia. Deposits in Sundaland that contain cervids are found in peninsular Thailand and Malaysia, Sumatra, Borneo, Palawan and Java, but are unevenly distributed. Although outside the scope of this review, deer fossils are also known from a number of sites in mainland Southeast Asia, which is in zoogeographical terms part of the Indochinese subregion. In this region Pleistocene sites with cervids are found in Northern-and Central Thailand (e.g. Auetrakulvit 2004, Tougard & Montuire 2006, Zeitoun *et al*. 2005, 2010, Conrad *et al*. 2013, Filoux *et al*. 2015, Suraprasit *et al*. 2016), Cambodia (Beden & Guérin 1973, Forestier *et al*. 2015), Laos (Bacon *et al*. 2008a, 2010, Demeter *et al*. 2010), Vietnam (e.g. Long *et al*. 1996, Bacon *et al*. 2006, 2008b, Rabett *et al*. 2011), Southern China (e.g. Wei 1957, Li 1961, Wang *et al*. 2007) and Myanmar (e.g. Pickford 2013, Aung *et al*. 2015). The following review will focus on the fossil deer of the Sundaic subregion, of which Java is part. A map with the sites mentioned in this review is given in Figure 4.4.

A number of excavations of prehistoric cave sites in Malaysian Borneo have since the 1960s provided evidence for the presence of cervids since at least the Late Pleistocene (Harrison 1998, Piper *et al*. 2008). The oldest records are from Niah cave in the Sarawak province (Medway 1964, Piper *et al*. 2008, Cranbrook 2010) and date back to about 45.000 Ka. Only

extant species are known from the Bornean records. At Niah cave (Piper *et al*. 2008) and Madai cave (Harrison 1998), also on the Malaysian part of the island, sambar (*Cervus* (*Rusa*) *unicolor*) and muntjac (*Muntiacus* cf. *muntjak*) were indentified. Evidence is absent from the Indonesian part of Borneo. The fossil record of Peninsular Malaysia is also poorly known. From the latter region Hooijer (1962) identified a possible large deer of the subgenus *Rusa* from the Middle Pleistocene site of Ipoh (Kinta Valley, Perak). Some more recently collected material from Perak and Sengalot -of uncertain age- contained fragments of *Cervus* (*Rusa*) *unicolor* (Ibrahim *et al.* 2012).

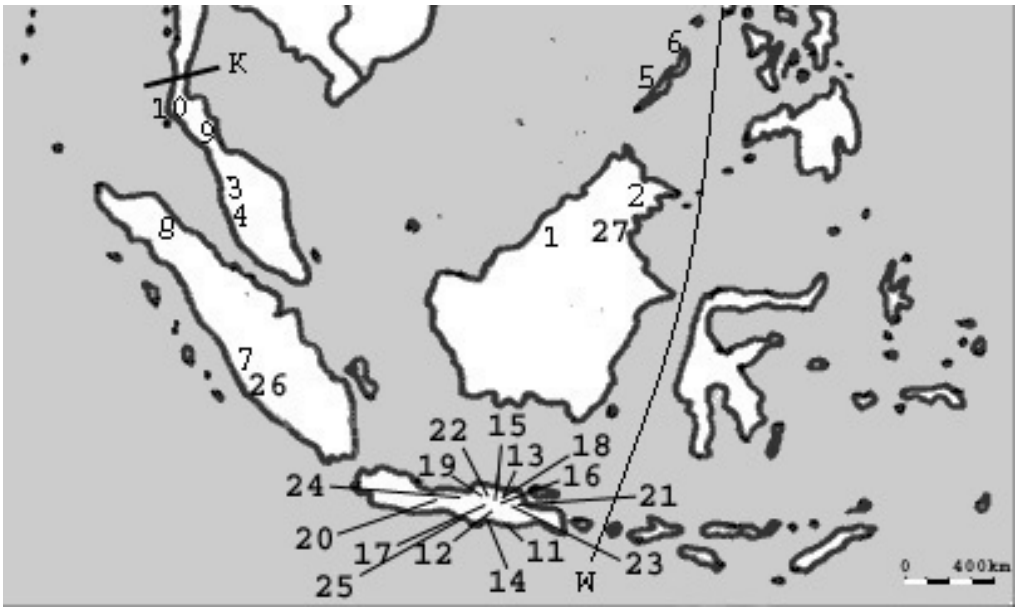


Figure 4.4: Quaternary sites in Sundaland with deer fossils mentioned in this chapter. 1. Niah cave, 2. Madai cave, 3. Ipoh, 4. Perak, 5. Tabon, 6. Ile cave, 7. Sibrambang-,Djambu- and Lida Ajer caves, 8. Binjaj Tamieng, 9. Thung Nong Nien, 10. Lang Rongrien, Moh Khiew I and II, 11. Wajak cave, Ketjil cave and Hoekgrot, 12. Sampung, 13. Ngandong, 14. Punung, 15. Trinil, 16. Kedung Brubus, 17. Watualang and Pitu, 18. Pandejan, 19. Sangiran, 20. Bumiaju, 21. Perning, 22. Baringinan, 23. Bangle, 24. Sembungan, 25. Braholo cave, 26. Tianko Panjang, 27. Hagop Bilo. K= Kra Isthmus, W= Wallace's line (as modified by Huxley).

Adjacent to Eastern Borneo lies the smaller island of Palawan which also forms part of the Sundaic biogeographical subregion (Reis & Garong 2001) and has an extant fauna broadly similar to that of Borneo. Here the fossil record goes back to the Late Pleistocene in Tabon (Fox 1970) and Ile cave (Piper *et al*. 2011). Fossils of at least two deer species are known from the island: a smaller species identified as *Axis* (*Hyelaphus*) *calamianensis* and a larger species identified as *Cervus* (*Rusa*) sp. The taxonomic classification of the latter remains unresolved, but metric data suggest an affinity with *Cervus* (*rusa*) *mariannu*s (Piper *et al*. 2011). Both taxa are extinct from the main island of Palawan today, although *Axis* (*Hyelaphus*) *calamianensis* is still present on the nearby smaller islands of Busuanga and Culion (Piper *et al*. 2011). In the Northernmost part of the Sundaic subregion, the Thai peninsula, only the remains of extant forms from the Late Pleistocene are present. Remains of *Muntiacus muntjak* and *Cervus* (*Rusa*) *unicolor* were found at Thung Nong Nien, Lang Rongrien and Moh Khiew I and II (Auetrakulvit 2004).

In Sumatra a number of cave deposits from the Padang Highlands have provided evidence of Pleistocene deer (de Vos 1983). The Sibrambang-, Djamboe- and Lida Ajer cave assemblages, thought to date from the early Last Interglacial (between 125 and 60 ka) (de Vos 1983, Westeway *et al*. 2007) contain deer remains. Taxa identified on these sites are: *Cervus* (*Rusa*) sp., *Muntiacus* sp. and *Muntiacus muntjak* (de Vos 1983, Gruwier *et al.* 2015). Similar to the cervids from other areas of Sundaland, the identification of the Rusa deer from Sumatra remains problematic, but morphometric data indicate a close match with *Cervus* (*Rusa*) *unicolor*, the Javan *Cervus* (*Rusa*) *timorensis* or its probable ancestor *Cervus* (*Rusa*) *kendengensis* (Gruwier *et al*. 2015). Some Late Pleistocene/Early Holocene fragments of *Cervus* (*Rusa*) cf. *unicolor* and *Muntiacus* sp. are known from Binjaj Tamieng, a prehistoric

shellmidden in Northern Sumatra (Schürmann 1928, Gruwier 2017). An unspecified large deer was described at Tianko Panjang (Bronson & Asmar 1975).

The palaeontological record of Java is probably the best known in the region (Louys *et al*. 2007). Many of the Pleistocene deposits on this island have yielded remains of cervids. This has led to a high number of species being described in the literature (e.g. von Koenigswald 1933, 1934) although some of these may be obsolete (Gruwier *et al*. 2015). In general the Javan fossil record is characterized by large sized deer of the genus *Cervus* (subgenus *Rusa*), medium sized deer that are generally assigned to the genus *Axis* and small sized species of the genus *Muntiacus* (Gruwier *et al*. 2015, Amano *et al*. 2016). The exact classification of these forms remains controversial. An overview of the taxa described from the palaeontological record of Java is given in Table 4.3.

All three species currently living in Java (*Axis* (*Hyelaphus*) *kuhlii*, *Cervus* (*Rusa*) *timorensis* and *Muntiacus muntjak*) are known from the fossil record. The Bawean deer (*Axis kuhlii*), which currently has a distribution limited to the small Bawean Island, north of Java, is thought to have had a wider historical range. It was at least present on the main island of Java during the Early Holocene, as testified by its presence in Wajak cave (van den Brink 1982, Simanjuntak & Asikin 2004). Its taxonomic affinities with the Pleistocene deer of Java are not well understood though. *Cervus* (*Rusa*) *timorensis* is certainly present in a number of Holocene cave deposits such as Sampung cave (Dammerman 1934), Wajak cave (van den Brink 1982, 1983) and Hoekgrot (Storm 1990). *Cervus* sp. described from the Late Pleistocene Punung (Badoux 1959, Storm & de Vos 2006, Westaway *et al*. 2007) probably belongs to this species and *Cervus hippelaphus* known from the Late Pleistocene locality of Ngandong (von Koenigswald 1934) should also be considered synonymous with this form.

	Taxon	Synonyms
Small sized taxa [genus *Muntiacus*]	*Muntiacus muntjak* (Zimmerman 1780)*	*Cervulus* sp. (Dubois 1908) *Cervulus kendengensis* (Stremme 1911) *Muntiacus muntjac kendengensis* (von Koenigswald 1933) *Cervus muntjak* (Zimmerman 1780)* *Cervus moschatus* (Blainville 1816)* *Cervulus moschatus* (Blainville 1816)* *Cervulus muntiacus typicus* (Ward 1910)* *Muntiacus bancanus* (Lyon 1906)*
	Muntiacus bumiajuensis (von Koenigswald 1933)	Unknown
Medium sized taxa [probably genus *Axis*]	*Axis Lydekkeri* (Martin 1888)	*Cervus lydekkeri* (Martin 1886, Vogel von Falkenstein 1910) *Axis axis* (Dubois 1891) *Cervus liriocerus* (Dubois 1907, 1908) *Cervus* (*Axis*) *lydekkeri* (Stremme 1911, Stehlin 1925, Von Koenigswald 1933, 1934)
	Axis javanicus (Von Koenigswald 1933)	*Cervus javanicus* (Von Koenigswald 1933,1934) *Axis sunda* (Kretzoi 1947)
	Axis (*Hyelaphus*)*kuhlii* (Temminck 1836)*	*Cervus kuhlii* (Haltenorth 1963)*
	Cervus zwaani (Von Koenigswald 1933)	Possibly junior synonym of *Axis lydekkeri* (Martin 1886)
	Cervus (Rusa) stehlini (Von Koenigswald 1933)	Unknown
Medium- to large sized taxon [(sub)genus uncertain]	*Cervus oppenoorthi* (von Koenigswald 1933)	According to Van Bemmel (1944) a junior synonym of *Axis* (*Hyelaphus*) *kuhlii* *
Large sized taxa [probably (sub)genus *Cervus*(*Rusa*)]	*Cervus* (*Rusa*) *timorensis* (de Blainville 1822)*	*Cervus hippelaphus* (Cuvier 1825)* *Cervus russa* (Muller & Schlegel 1885)* *Cervus timorensis russa* (Muller & Schlegel 1885)* *Cervus peronii (*Cuvier 1825)* *Cervus tavistockii* (Lydekker 1900)*
	Cervus kendengensis (Dubois 1908)	Unknown
	Cervus palaeomendjangang (Dubois 1908)	Possibly junior synonym of *Cervus kendengensis* (Von Koenigswald 1933)
	Cervus problematicus (von Koenigswald 1933)	Unknown
	Cervus sp. (Martin 1888)	Unknown
	Cervus (Dubois 1907)	Unknown
	Cervus (*Rusa*) sp. (Dubois 1892)	Unknown
	Cervus (*Rusa*) sp. (Von Koenigswald 1933)	Unknown
	Cervus sp. (Stehlin 1925)	Unknown
	Cervus sp. (Von Koenigswald 1933)	Unknown
	Cervus (*Rusa*) sp. (Aziz & De Vos 1999)	Unknown
	Cervus sp. (Stehn & Umgrove 1926)	Unknown

*Table 4.3: Taxa known from the Javan fossil record by size category. *= described from extant form.*

Dammerman (1934) mentioned the presence of *Cervus* (*Rucervus*) *eldii* in the Holocene of Java based on the presence of one antler fragment from Sampung cave. This specimen was described by the author as peculiar in morphology due to the fact that the brown tine forms an almost continuous curve with the beam. Von Koenigswald (1933) did however describe similarly shaped antlers from Nandong and considered them as belonging to a subspecies of *Cervus* (*Axis*) *javanicus*. As such a morphology is apparently not unique to *Cervus eldii* and given its further absence from the rest of Sundaland, the presence of this species in Java is unlikely.

Fossil remains of muntjacs from the Quaternary of Java have for the most part been identified as the extant red muntjac (*Muntiacus muntjak*). Holocene red muntjacs are known from a number of cave sites such as Ketjil cave (Span 1993), Wajak cave (van den Brink 1982), Braholo cave (Amano *et al*. 2015) and Hoekgrot (Storm 1990). From the Late Pleistocene its presence is mentioned at Ngandong (von Koenigswald 1933), from the Punung deposits (Badoux 1959) and from the Late Pleistocene/Holocene Braholo cave (Amano *et al*. 2015). Other Pleistocene fragments of this species were found at Pandejan, Watugudel (Pitu), Bangle, Kedung Brubus, Sembungan (von Koenigswald 1933) and Sangiran (von Koenigswald 1934).

A possibly extinct species of muntjac (*Cervulus*/*Muntiacus kendengensis*) was described from the Early/Middle Pleistocene sites of Trinil and Pandejan based on a small number of antler fragments (Stremme 1911, von Koenigswald 1933). According to Stremme (1911) the antlers of this form were sufficiently different in size and morphology to separate it from the extant red muntjac (*Muntiacus muntjak*). Von Koenigswald (1933) on the other hand considered it merely a subspecies of the recent form (*Muntiacus muntjak kendengensis*). The only extinct muntjac recognized by von Koenigswald was a new species from the Early Pleistocene of

Bumiaju: *Muntiacus bumiajuensis* (von Koenigswald 1933). This form was described on the basis of a single maxillary fragment (von Koenigswald 1933).

Of the medium sized deer of Java, probably one of the most common species in the fossil record is *Axis lydekkeri* (Martin 1888). This form was described on the basis of an almost complete, smooth, groove-less antler with a typical lyre-shape (Martin 1888, Zaim *et al*. 2003). The type specimen most likely belongs to a subadult (Dubois 1908). *A. lydekkeri* is relatively well known and identified from the fossil record by a number of researchers (Dubois 1908, Vogel von Falckenstein 1910, Stremme 1911, von Koenigswald 1933, 1934). Although in the initial description it was already realized that its morphology was different from any extant species (Martin 1888), it was Dubois (1908) who pointed out its similarity to the Indian Chital (*Axis axis*). Meijaard and Groves (2004) classify it under the subgenus *Hyelaphus*, which is confirmed by a more recent morphometric study (Gruwier *et al*. 2015). *Axis lydekkeri* is abundant in Trinil (von Koenigswald 1934), but also present in other sites such as Kedung Brubus (von Koenigswald 1934), Pitu, Watualang (von Koenigswald 1933) and Sangiran (Moigne *et al*. 2004a, 2004b). According to Zaim and colleagues (2003) it is similar in size to *Axis* (*Hyelaphus*) *porcinus* and Vogel von Falckenstein (1910) mentions that it is somewhat smaller than *Axis axis*. Both these statements are confirmed by recent morphometric research (Gruwier *et al*. 2015).

Another medium sized species of the same genus, but without a clearly assigned type specimen, is *Axis javanicus* (von Koenigswald 1933, 1934). Many antler fragments from the Late Quaternary are placed under this taxon (Zaim *et al*. 2003). It is best known from the Late Pleistocene at Ngandong (von Koenigswald 1933) in addition to Watualang, Pandejan and possibly Pitu (Zaim *et al*. 2003). Characteristic for this species are slightly pearled antlers with an angle between the beam and the brown tine of more than 90 ° and usually with an

accessory tine within this angle (von Koenigswald 1933, Zaim *et al*. 2003). Moigne (2004a) argues this species is most similar to *Axis* (*Hyelaphus*) *kuhlii*, and might be considered a subspecies of the latter. Meijaard and Groves (2004) on the other hand consider it synonymous with- or closely related to- a form of the extant chital (*Axis axis*) that migrated from the mainland to Java during the Late-Pleistocene.

A species of intermediate size described by von Koenigswald (1933) is *Cervus zwaani*. This taxon is based on four mandibles and an upper third molar from the Early Pleistocene of Bumiaju in Western Java. In addition some fragments from Perning (von Koenigswald in de Terra & Patterson 1939, de Terra 1941), Sangiran and Baringinan (von Koenigswald 1934) were also provisionally attributed to this species. No antlers have been attributed to *Cervus zwaani* (Zaim *et al*. 2003), but according to von Koenigswald (1933) it was slightly larger and had more robust premolars than *Axis lydekkeri*. Later studies (Zaim *et al*. 2003, Gruwier *et al*. 2015) did however not find any substantial metric or morphological differences between *Cervus zwaani* and *Axis lydekkeri*. It is not unlikely that *C. zwaani* is a junior synonym of *A. lydekkeri*.

Besides these animals of intermediate size, generally assigned to the genus *Axis*, there are a high number of large deer, usually attributed to the genus genus *Cervus* and subgenus *Rusa*. One of the better known taxa is *Cervus kendengensis* (Dubois 1908). Dubois (1908) thought *C. kendengensis* was similar to the recent *Cervus hippelaphus* (now *Cervus* (*Rusa*) *timorensis*) but considered it a separate species due to its shorter and thicker antlers. Although Dubois (1908) gave a short description of this species and many fossils from the Middle Pleistocene sites of Bangle and Kedung Brubus in the collection of Naturalis were placed by him under this taxon, no type specimen was designated. In the same publication, Dubois (1908) also described another new species: *Cervus palaeomendjangan*. This second large cervid was

characterized by the peculiar morphology of its antlers with typically small tines pointing outwards and to the front, similar to the recent large Javan deer (*Cervus* (*Rusa*) *timorensis*) (Dubois 1908). This species was however not recognized by von Koenigswald (1933).

Another large sized species is *Cervus stehlini*. This form was described on the basis of several mandibles and a small number of antler fragments from the Early Pleistocene of Bumiaju (von Koenigswald 1933). Von Koenigswald (1933) considered it a separate species from *Cervus hippelaphus* (now *Cervus* (*Rusa*) *timorensis*) based on the morphology and slenderness of its premolars. Besides these small differences however, the author considered it similar in shape and size to the living rusa deer from Java (*Cervus* (*Rusa*) *timorensis*).

Cervus (*Rusa*) *oppenoorthi*, a species of unclear taxonomic status, is known from a number of antler fragments from Pitu and Sembungan (von Koenigswald 1933). Von Koenigswald (1933) noted that its antlers were strongly pearled and similar in morphology to the recent *Axis* (*Hyelaphus*) *kuhlii*, but larger in size. He considered it distinct from *Axis lydekkeri* and the Javan Rusa deer (*Cervus* (*Rusa*) *timorensis*) and probably most closely related to *A*. *kuhlii* (von Koenigswald 1933). This point of view was shared by van Bemmel (1944) who even considered it a subspecies of *A. kuhlii*. Zaim and collegues (2003) on the other hand have argued that it was probably more closely related to the *Rusa*-subgenus. It should be noted that at the time von Koenigswald classified these specimens, the Bawean deer (*Axis* (*Hyelaphus*) *kuhlii*) was placed in the subgenus *Rusa* (von Koenigswald 1933). Moreover, the taxonomic status of the subgenus *Hyelaphus* remains unresolved to this day and some recent molecular studies have supported a close relationship between the subgenus *Hyelaphus* and the *Cervus* (*Rusa*) *timorensis*/*Cervus* (*Rusa*) *unicolor*-clade (Pitra *et al*. 2004).

The largest form recognized in the Pleistocene record of Java is *Cervus* (*Rusa*) *problematicus*. It is known from a partial cranium and a lower first molar from the Early Pleistocene of Bumiaju (von koenigswald 1933). Later von Koenigswald (1934) included other remains in this taxon and placed it under the subgenus *Rusa*. In addition, the skull fragment from Bumiaju, was recently re-identified as a bovid and should be excluded from this species (van den Bergh in Zaim *et al*. 2003). The tooth fragment on the other hand appears to be properly identified as a large sized cervid (personal observation).

Von Koenigswald (1933) also described several large forms from the fossil record which he did not assign to a species. It is unclear whether these finds should be considered separate taxa from the ones already mentioned. A badly preserved antler fragment was identified as *Cervus* sp. (von Koenigswald 1933) and a partial skull with antlers from Sembungan was classified in the same publication as *Cervus* (*Rusa*) sp. (von Koenigswald 1933). The author noticed that it was similar to *Cervus* (*Rusa*) *timorensis* and *Cervus* (*Rusa*) *unicolor*, but due to its unusual morphology and the sharp kink in the skull profile he refrained from giving it a more specific classification (von Koenigswald 1933).

In addition to von Koenigswald, a number of other researchers also noticed the presence of larger sized deer in the Javan fossil record without assigning them to a species. Martin (1888) mentioned that there was a larger deer (*Cervus* sp.) present in the then known collections besides the smaller axis-like deer. Dubois (1891) came to the same conclusion and observed at least two different deer amongst the fossils he had collected in the field. In addition to *Axis lydekkeri*, there was a larger, rarer species with heavier antlers that was reminiscent of *Cervus* (*Rusa*) *timorensis* and to some extent also to *Cervus* (*Rusa*) *unicolor* (Dubois 1891, 1907). In the absence of a type specimen it is unclear which fossils the author was referring to. Other

large sized deer of unclear taxonomic affinity include *Cervus* sp. sensu Stehlin (1925), *Cervus* sp. sensu Stehn and Umgrove (1929) and *Cervus* (*Rusa*) sp. sensu Aziz and de Vos (1999)

4.5 Cervids in ecomorphology

While some ecomorphological studies of bovids have included some cervid specimens in their extant training set (Kovarovic 2004, Schellhorn 2009, Schellhorn & .Pfretzschner 2015) so far only Curran's (2009, 2012, 2015) work has specifically focused on the cervid family. There are a number of reasons why cervids are an appropriate subject for palaeoecological studies similar to those based on bovid ecomorphology.

First of all, cervids are members of the artiodactyl order, like the suids and bovids that have both already proven to be useful palaeoenvironmental proxies in ecomorphological studies (e.g. Kappelman 1988, Bishop 1994, Bishop *et al*. 2006, Kappelman *et al.* 1997, Vrba 1980, 1995b, 1999, Plummer & Bishop 1994, Degusta & Vrba 2003, 2005a, 2005b, Scott 2004, Weinand 2005, Kovarovic & Andrews 2007, Cuddahee 2008, Plummer *et al*. 2008, Schellhorn 2009, Klein *et al*. 2010, Barr 2014a, Forrest *et al.* 2018). There are indications that, similar to other ruminants, predator evasion strategy is also the main selective constraint on cervid postcranial morphology (Geist 1998, Curran 2009). On a higher taxonomic level it should be added that most of the differences in (limb) morphology between cervids and bovids are probably the result of adaptation to different environments (Leinders 1979). There are indications that the same principle also applies within the cervid family (Janis 2007, Curran 2009).

Cervids are a widely distributed family that is characterized by a high number of species that have adapted to a range of environments (Putman & Flueck 2011). Although the environmental flexibility of cervids is not of the same magnitude as that found in bovids

(Geist 1998, Janis 2007), they are expected to show a similar morphological variation to that seen in bovids adapted to different kinds of environments. As deer tend to be more generalistic in their behaviour than bovids (Geist 1998) it is predicted that this is also reflected in their osteomorphology. Ecomorphological differences are expected to be more subtle than in bovids but of the same nature.

Deer having originally evolved in Asia, never managed to successfully colonize most of Africa, apparently being unable to overcome the geographical barriers that the Sahara and the Nile Delta posed (Tchernov 1992, Geist 1998). The reasons for this are unclear, especially as bovids *did* manage to disperse over most of Africa and Eurasia (Goss 1983, Geraards 2010). In any case, the range of niches occupied in Africa by a diversity of bovids, is in Eurasia to a large extent occupied by cervids (Geist 1998). It is known that in regions where bovids and cervids are sympatric, niches that have opened up (e.g. as a result of extinction) are often reoccupied by members of the other group (Leinders 1979). Consequently fossils of cervids are a common element in European and Asian palaeontological and archaeological assemblages (Curran 2009). In that sense such fossils can serve as valuable palaeoecological proxies in the same way as bovids can for African Pleistocene sites.

5. Hypotheses, methods and materials

5.1 Research questions and hypotheses

In chapter 3 I discussed how *Homo erectus* was the first hominin able to expand its biogeographic range over large parts of Africa and Eurasia (Anton & Swisher 2004). The underlying causes for this event are not well understood, but it is likely that a combination of extrinsic (i.e. environmental) and intrinsic changes (i.e. behavioural and/or morphological) in and around *Homo erectus* allowed it to disperse into new areas (Carotenuto *et al.* 2016). It is nevertheless unclear whether intrinsic or extrinsic factors played a more decisive role in early *Homo* dispersal.

This dissertation addresses this question by looking at the palaeoecology of hominin sites in Southeast Asia and elsewhere. By comparing palaeoenvironmental reconstructions of different *Homo erectus* sites, an estimate can be made of the adaptive flexibility of this species. If reconstructions point to a relatively specific and uniform type of environment (e.g. savannah-like environment) for all sites, the data would support a scenario where extrinsic changes in the landscape primarily drove early hominin expansion and success. If palaeoenvironmental reconstructions point to a range of different environments that *Homo erectus* occupied, the data would support a scenario where intrinsic changes (perhaps as a result of variability selection) made *Homo erectus* a flexible species that was less restricted by specific ecological parameters in its dispersal over larger parts of the Old World.

The palaeoecological analyses in this dissertation are therefore not merely for the sake of providing insight into the regional conditions that were present in Java during the Pleistocene, but should ultimately be considered as a test of the above outlined theories concerning hominin dispersal. By presenting new palaeoecological data based on ecomorphological

analyses of Indonesian Pleistocene cervids and by examining them in conjunction with data from other palaeoecological proxies and from other sites, a contribution is made to our understanding of the capacity for environmental flexibility in *Homo erectus*.

More specifically cervid fossils from several sites in Java, associated with two biostratigraphic units (the Trinil H.K. and the Kedung Brubus faunal units), are subjected to ecomorphological analyses. The island of Java forms the ideal test case for such an analysis for a number of reasons. First, because it lies at the easternmost limit of the *Homo erectus* range and despite being rich in hominin fossils, the palaeoecology of this area has not been as well studied compared to that of East Africa and Europe. As some of the currently available palaeoecological data is conflicting (e.g. van den Bergh et al. 2001, Louys 2007), alternative approaches such as ecomorphology, can make an important contribution to settling disputes surrounding the nature of the Pleistocene environments of Java. A second advantage is that, contrary to many African sites, there is less doubt about the identification of the human fossils from this region. As *Homo erectus* is currently thought to be the only Early to Middle Pleistocene hominin present on the island (Dunsworth & Walker 2002), there is little chance of confusion with other members of the genus (although see Zanoli *et al*. 2019). And finally, as was already discussed in detail in Chapter 2, the fossil record of Java is exceedingly rich and has a long history of palaeontological research (e.g. Dubois 1907, 1908, von Koenigswald 1933, 1934, 1935). This has resulted in large collections of faunal remains found in association with *Homo erectus*, providing sufficient materials for robust quantitative analyses.

An important aspect about the Trinil H.K. (0.9 Ma) and the Kedung Brubus biostratigraphic units (0.7-0.8 Ma) (van den Bergh *et al.* 2001) is that there are indications that the transition between these successive phases may correspond to significant climatic and environmental changes. This is indicated by the appearance of a range of new vertebrates and the possible

coincidence of the Kedung Brubus fauna with a glacial maximum and extremely low global sea levels (Musser 1982, Sondaar 1994, Meijaard 2003a). Most important for this study is the appearance in the younger levels of one or more new cervid species (e.g. *Cervus* (*Rusa*) *kendengensis*). Despite these observations, the palaeoenvironmental changes that took place in the region during this transition are not well known. This supposed coincidence with a glacial stage and influx of new species from the continent could imply that Kedung Brubus represented a more arid phase than Trinil H.K. While certain researchers (Weinand 2005) have found evidence for such an aridification, others have merely seen a continuation of the general conditions present during the deposition of the Trinil H.K. fauna (van den Bergh et al. 2001).

By using cervid fossils from sites that are associated with these biostratigraphic units it is possible to generate new palaeoenvironmental interpretations that will allow for a more detailed insight into the changes that took place in Java during the Early and Middle Pleistocene. This will lead to a better understanding of what role *Homo erectus* played in these ancient ecosystems and indirectly provide clues about the extent to which extrinsic environmental conditions constrained its biogeographic distribution.

In order to gain a more detailed understanding of the nature of Javan palaeoenvironments by means of ecomorphological analysis, it is first necessary to develop a functioning model based on extant species of known ecological preference. Developing such a predictive model that can be applied on fossil cervids is a goal in itself because it can also be used on specimens from other palaeontological sites, as long as the appropriate skeletal elements are present. In this case a model was constructed for the calcaneus and the intermediate phalanx. As part of the development of this model, a number of hypotheses will be tested that specifically deal with the relationship between certain morphological traits in these elements

and ecological parameters. The specific hypotheses with respect to the functional and ecological morphology of the cervid lower limb are presented in section 5.2, but in general the main research questions dealing with hominin behaviour and palaeoecology in this dissertation are the following:

- What environmental conditions were present around the Early and Middle Pleistocene sites where *Homo erectus* was found, as suggested by the cervid ecomorphological analyses?

- Were there any significant differences between the older Trinil H.K. biostratigraphic unit and the younger Kedung Brubus unit? If this is the case, can these differences be reconciled with current palaeoclimatological and palaeoecological data from the region? Is there for example a shift towards more arid environments that could be linked to regional or global climatological events?

- Was *Homo erectus* in Java only found in one specific type of habitat or was it able to adapt to significant environmental change? Does the data perhaps suggest that *Homo erectus* was associated with a open (savannah-like) environments or was the presence of an aquatic component a necessary condition?

- To what extent do these findings support or refute current models about early hominin palaeoecology and dispersal?

5.2 Functional morphology and biomechanics of the cervid limb

In order to develop an ecomorphological model for the cervid intermediate phalanx and calcaneus it is important to start from a number of hypotheses that predict the relationship

between morphological characteristics and ecological variables that are firmly rooted in ecological and biomechanical theory (Bock 1994, Cuddahee 2008, Curran 2009). Although limited research has been conducted on cervid functional morphology and biomechanics, by combining theory from the existing literature on ecologically and morphologically similar bovids (e.g. Kappelman 1988, Kappelman *et al.* 1997, Scott 2004), artiodactyls (e.g. Leinders 1979, Köhler 1993) and other mammalian groups (e.g. Polly 2007, 2008, Warburton & Prideaux 2010, Galvez-Lopez & Casinos 2012, Scarborough *et al.* 2016), valuable hypotheses can be formulated and their viability explored.

The calcaneus and intermediate phalanx are thought to be suitable for such analyses as previous research on artiodactyls has already demonstrated that their morphology is correlated with vegetation and substrate type (e.g. Degusta & Vrba 2003, 2005a, 2005b, Kovarovic 2004, Kovarovic & Andrews 2007, Schellhorn 2009, Barr 2018). Moreover there are indications that the two elements may be, at least partially, driven by different ecological parameters. The morphology of the calcaneus is considered to be more influenced by vegetation type (Curran 2009, Barr 2018), while the shape of the intermediate phalanx may covary more with substrate type (Curran 2009). Consequently, they can be complementary in palaeoenvironmental reconstructions. Although these assumptions will be further explored in this chapter, they played a role in the initial selection of these elements for ecomorphological analysis. A third reason for choosing these elements was their availability in the fossil record. Smaller, more compact elements have a higher chance of survival due to their density and because they are less attractive to scavengers (Borerro 1990). This is not different for Indonesian palaeontological assemblages and intact calcanei and phalanges are fairly common in the sites studied in this dissertation.

The calcaneus and intermediate phalanx are both part of the lower hindleg. As the extant ecomorphological models developed here are primarily based on posterior phalanges and because the anterior and posterior phalanges are serially homologeous in ungulates (Hanot *et al.* 2017), the emphasis will be on describing this element as part of the hindfoot. The bone structure of this part of the leg in deer is similar to that found in domestic cattle (*Bos taurus*) (Getty 1986, Schimming *et al*. 2015). It comprises the tarsus, metatarsus and posterior phalanges (Schimming 2015) (Fig. 5.1). The tarsus is composed of a proximal and a distal row (Rajani *et al*. 2013, Schimming *et al*. 2015). The proximal row contains the calcaneus and the astragalus, with the cubonavicular (fused central tarsal and fourth tarsal bone) and the small and large cuneiform bones in the distal row (Rajani *et al.* 2013). The metatarsus is characterized by fusion of the third and the fourth metatarsal bones into a sturdy cannon bone while the second and fifth metatarsals are absent in the hind legs (Geist 1998). In the front legs the second and fifth metacarpals (not shown in figure 5.1) are still present in a vestigial state (Brooke 1878, Geist 1998). In New World deer and musk deer these vestigial metapodials are reduced to distal splinters medio-lateral to the cannon bone (the telemetacarpalian condition), while in Old World deer they are reduced to proximal splinters (the plesiometacarpalian condition) (Geist 1998, Groves 2007).

Deer have four fingers in the hind legs, two of which are well developed and touch the ground (digits III and IV), while the other two (digits II and V) are vestigial (Rajani *et al.* 2013, Schimming *et al.* 2015). Each digit is composed of three phalanges of different lengths, the proximal (or first) one being the longest and the intermediate one (or second) being about one third the size of the former (Rajani *et al*. 2013). The distal (or third) phalanx is the shape of a hoof and has a sharp dorsal border (Rajani *et al*. 2013, Schimming *et al.* 2015).

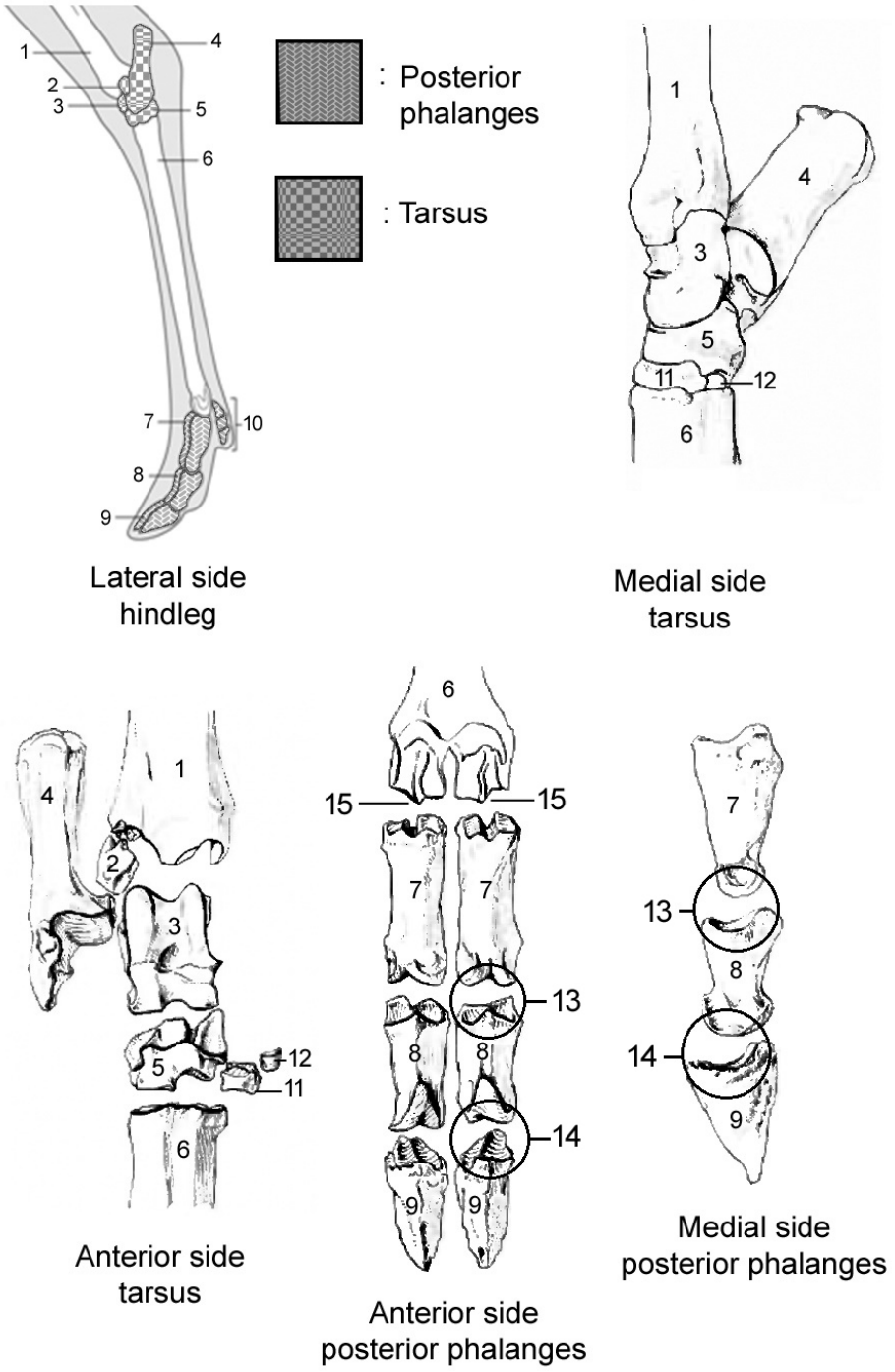


Figure 5.1: The cervid hindfoot (adapted from Ferrié 2005 and Pales & Garcia 1981). 1:Tibia, 2:Malleolus, 3:Astragalus, 4:Calcaneus, 5:Cubonavicular, 6:Metatarsus, 7:proximal (first) phalanx (digits III & IV), 8:Intermediate (second) phalanx (digits III & IV), 9:Distal (third) phalanx (digits III & IV), 10:Vestigeal phalanges (digits II & V), 11:Large cuneiform bone, 12:Small cuneiform bone, 13:Proximal interphalangeal joint, 14:Distal interphalangeal joint, 15: Metapodial verticillus.

Deer have four fingers in the hind legs, two of which are well developed and touch the ground (digits III and IV), while the other two (digits II and V) are vestigial (Rajani *et al.* 2013, Schimming *et al.* 2015). Each digit is composed of three phalanges of different lengths, the proximal (or first) one being the longest and the intermediate one (or second) being about one third the size of the former (Rajani *et al*. 2013). The distal (or third) phalanx is the shape of a hoof and has a sharp dorsal border (Rajani *et al*. 2013, Schimming *et al.* 2015).

The intermediate phalanx

The intermediate phalanx proximally articulates with the distal articulation of the proximal phalanx and distally articulates with the third phalanx. The main movement of the proximal interphalangeal joint is volar flexion of the intermediate phalanx, while the distal interphalangeal joint (Fig. 5.1) permits dorsal and volar flexion (Leinders 1979).

According to Köhler (1993) and Leinders (1979) interspecific variation in phalangeal morphology is to a large extent driven by ecological differences such as vegetation and/or substrate type. These variations are also mirrored in the wider difference between cervids on the one hand and medium sized open landscape bovids on the other hand (Leinders 1979). Morphological differences between cervids and bovids are described in a number of works that deal with the morphology of these animals (e.g. Heintz 1970, Schmid 1972, Leinders 1979, Prummel 1988), albeit not necessarily all from a functional or ecological morphological perspective. Other works are more specifically concerned with the relationship between specific morphotypes and ecological variables (e.g. Köhler 1993, Degusta & Vrba 2005a). As the functional explanations underlying the morphological differences between intermediate phalanges are sometimes contradictory, I first present an overview of the observed differences across species of different habitat types, based on the literature and on personal observations.

Then I will consider the functional explanations that are thought to be at the basis of these differences.

A first notable osteomorphological difference observed in the phalanges between open environment species and those living in closed environments is the depth of the metapodial verticillus in the proximal articular surface of the first phalanx (Köhler 1993) (Fig. 5.1). This incision is deeper and more stable in species adapted to dry/open habitats. In wet/closed environment taxa it appears to be shallower and to allow for more medio-lateral movement (Köhler 1993).

Another difference observed by Köhler (1993), is that there is a high degree of variation in the general robusticity of the phalanges. These elements are thought to be more robust in closed/wet environment species than in open/dry environment forms (Köhler 1993). The opposite is, however, stated by Degusta and Vrba (2005b), who interpreted the greater relative length of the phalanx in the bovid *Tragelaphus spekii* as an adaptation to closed, swampy terrain. My examinations confirm high variability in robusticity between species, but a clear relationship with environment type could not be established from preliminary qualitative observations.

Köhler (1993) also described several other differences on the proximal side of the phalanges (Fig. 5.2). The proximal articular surface is more strongly concave in species of open/dry habitat, while it is flatter in species adapted to wet/closed environments. This is probably allows for more medio-lateral movement in wet/closed environment taxa. In addition, there are also substantial differences in the size of the plateau postarticulaire of the proximal articulation. In open/dry adapted species its anterio-posterior length is shorter than in species adapted to wet/closed environments (Köhler 1993).

A difference on the distal articulation of the intermediate phalanx is the placement of the extensor process on the anterior side (Fig. 5.2). According to Köhler (1993) it is extended towards the proximal side of the bone in species adapted to dry/open environments and closed to the distal side in animals adapted to closed/wet environments. The same may be the case for the palmar extensions on the posterior side of the phalanx. They are extended further towards the proximal side in dry/open adapted species and vice-versa. Furthermore, the shape of the outline of the distal articulation is also different between ecotypes. It is round in wet/closed forms and more oval with an apex pointing towards the posterior side in dry/open adapted forms (Köhler 1993). Mountain species are similar in shape to open/dry adapted species, but less slender in overall shape and the distal articular surface is more square-shaped than round (Köhler 1993).

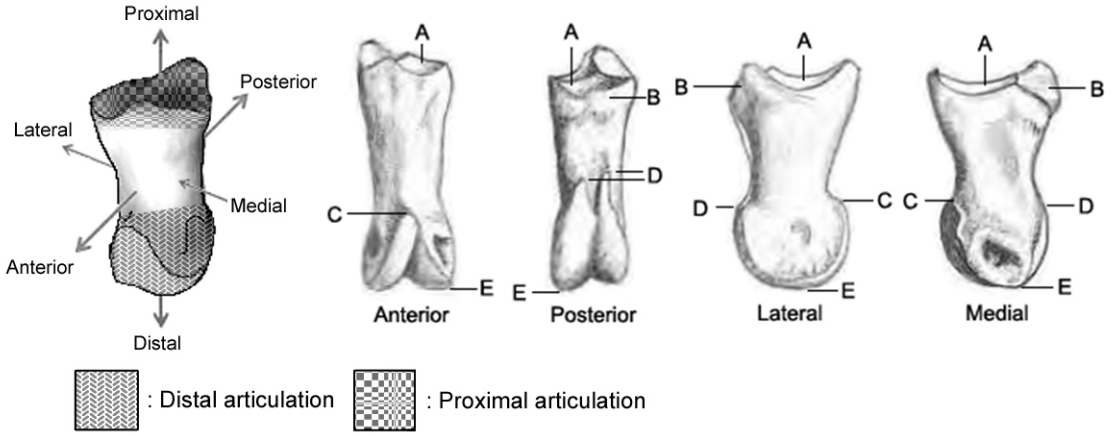


Figure 5.2:Anatomical terms of location and parts of the intermediate phalanx. A: proximal articular surface; B: plateau postarticulaire; C: extensor process on anterior side; D: palmar extensions on posterior side; E: distal articular surface (adapted after Köhler 1993).

While the above morphological variations are explicitely tested in a more quantitative way in chapter 6, the underlying explanations that link phalangeal morphology via function to ecology first need further exploration. Two key functional models are of importance with

respect to artiodactyl phalangeal morphology. A model developed in the 1970's by Leinders (1979) focuses heavily on the mechanical advantages of certain morphological adaptations in relation to jumping behaviour and shock absorption capacity, which he considers substantially different between open adapted species and closed environment species. A later model by Köhler (1993) is related to that of Leinders, but puts more weight on substrate type. She argued that differences in morphology are primarily adaptations that allow for more or less flexibility in the joints depending on the terrain on which the animal moves (Köhler 1993).

In Leinders' (1979) model the elastic properties of the tendo interosseus and its advantage in vertical and horizontal jumping is emphasized. Ruminants are characterized by a tendonified musculus interosseus. This so called tendo interosseus, or suspensory ligament, originates in the proximal metatarsus, connects the proximal sesamoids and inserts into the proximal phalanx. It continues through the plateau postarticulaire of the proximal phalanx until the plateau postarticulaire of the intermediate phalanx. During locomotion the tendo interosseus supports the metapodial-phalangeal joint and while running or jumping it prevents the phalanges from excessive flexion (Leinders 1979). The tendonification of this muscle provides a mechanical advantage due to its increased elastic properties. As a result of this added elasticity each dorsal flexion triggers a spring-like response whereby the foot bones are automatically placed in their original position again (Leinders 1979) (Fig. 5.3). This mechanism is better known in horses where it is called the pogostick mechanism (Sondaar 1968, Leinders 1979).

This pogostick mechanism is not equally developed in all ruminants (Leinders 1979). Cervids as well as goat-like bovids are considered "obstacle jumpers" in this model, as they both have the ability to jump over obstacles that are found in their typical (more closed) environments (Grzimek 1968, Leinders 1979). Contrarily, ruminants that live in open environments are

characterized by a different locomotor behaviour. These forms typically make long horizontal jumps when running at high speed and make so-called “stotting jumps”, vertical leaps in the air that are used when in danger (Leinders 1979). Although open-habitat species are capable of making impressively long jumps, they are hesitant to jump over obstacles (Leinders 1979).

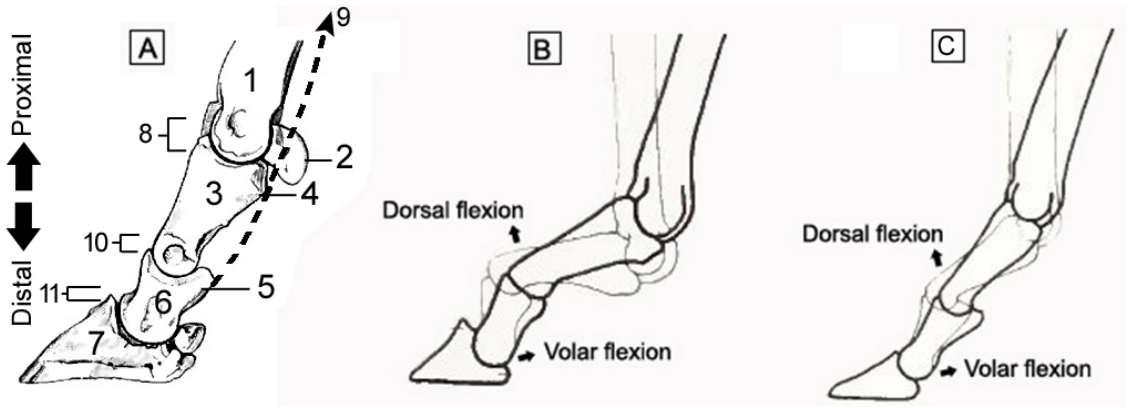


Figure 5.3: The pogostick mechanism. A:medial view of the elements responsible for the pogostick mechanism, with the tendo interosseus or suspensory ligament as a black dotted line (1=metatarsus, 2=proximal sesamoid, 3=proximal phalanx, 4=plateau postarticulaire of proximal phalanx, 5=plateau postarticulaire of intermediate phalanx, 6=intermediate phalanx, 7=distal phalanx, 8=metapodial-phalangeal joint, 9=to proximal metatarsus, 10=proximal interphalangeal joint, 11=distal interphalangeal joint); B: open habitat species with strongly developed pogostick mechanism; C: closed habitat species with weakly developed pogostick mechanism (thin black lines=neutral position of the foot bones, thin grey lines= flexed position of the foot bones) (adapted after Leinders 1979 and Pales and Garcia 1981).

These behavioural differences are reflected in the morphology of the lower limb (Leinders 1979) (see Fig. 5.3). By allowing greater dorsal flexion of the proximal interphalangeal joint and greater volar flexion of the distal interphalangeal joint, a higher shock absorbing capacity is achieved, which is especially advantageous for animals living in open landscapes that make long jumps and need to be able to quickly come to a stop when running at full speed. It is especially useful during zig-zag leaping at high speed in open plains (Leinders 1979). Furthermore, this adaptation is mostly useful on hard substrates (Leinders 1979). In the lower

leg this is reflected in a number of osteological traits such as the proximal extension of the articular surface of the distal metatarsus, allowing for more dorsal flexion in open adapted species. In the intermediate phalanx a difference is seen in the development of the so called plateau postarticulaire. In open adapted species the plateau behind the proximal articular surface is reduced, allowing the further volar flexion of the intermediate phalanx (Leinders 1979) (see Figures 5.2 and 5.3). In large bovids these jumping adaptations are less developed according to Leinders (1979), as jumping abilities are restricted by weight in these animals.

Köhler (1993) dismissed the notion that the main functional differences in the phalanges are related to shock absorption. She argued that most "good jumpers" are found in wooded habitats and that those species would especially need an increased ability to absorb shocks produced by the impact of jumping (Köhler 1993). According to Köhler (1993), animals adapted to closed environments have another way of absorbing the shock produced by vertical jumping. A spring effect is mainly created by volar flexion of the proximal phalanx on the metapodial-phalangeal joint (see Figures 5.2 and 5.3), while the intermediate- and distal phalanx stay in their neutral position. The interphalangeal flexion seen in open environment species is more related to "breaking" in the horizontal plane. In Köhler's (1993) functional model, however, splaying of the phalanges explains the main functional difference in the morphology of the digits (Fig. 5.4). Animals adapted to open plains that run at high speed have railed articulations between the metapodial-phalangeal joint and between the interphalangeal joints, preventing them from disarticulating. Species that live on more difficult substrates such as those found in mountainous or wet areas, allow more medio-lateral movement (splaying) of the articulations for stability (Köhler 1993). In this model predator evasion is less emphasized (Scott 2004), although it is likely that these adaptations would be of most use when escaping a predator at high speed.

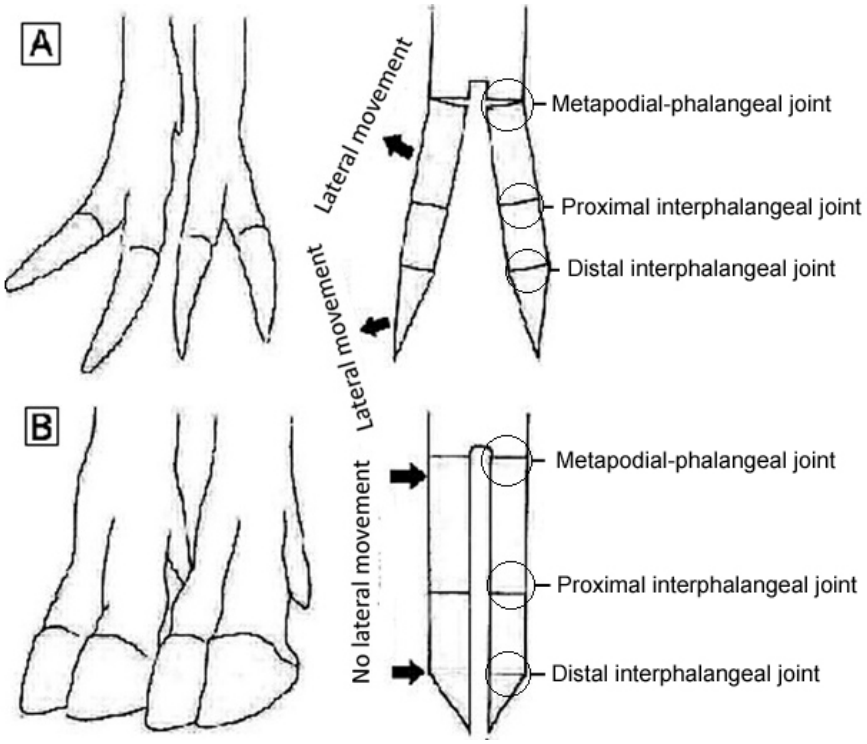


Figure 5.4: Splaying of phalanges; A: Species adapted to wet/forested environment with phalanges that allow medio-lateral splaying; B: Species adapted to open/dry environment with railed phalanges that do not allow medio-lateral movement; (adapted after Köhler 1993).

The calcaneus

The calcaneus is the largest tarsal bone in cervids and consists of an anterior portion that articulates with the astragalus, the os malleolus and cubonavicular and a posterior part: the tuber calcanei (Lessertisseur & Saban 1967, Curran 2012) (Fig. 5.5). Together with the articulations between the tibia and astragalus, and between the astragalus and cubonavicular, it forms the hock joint (Curran 2012). While the astragalus functions as a hinge point between the tibia and the metatarsus (Barr 2014), the calcaneus acts as the lever for the calf muscles that insert into the tuber calcanei via the achilles tendon (Galvez-Lopez & Casinos 2012). Being mostly restricted to movement in the sagittal plane (Schaeffer 1947), the calcaneus pushes the limb against the ground and causes the animal to advance during locomotion when the calf muscles contract (Alexander 1983, Galvez-Lopez & Casinos 2012, Curran 2012).

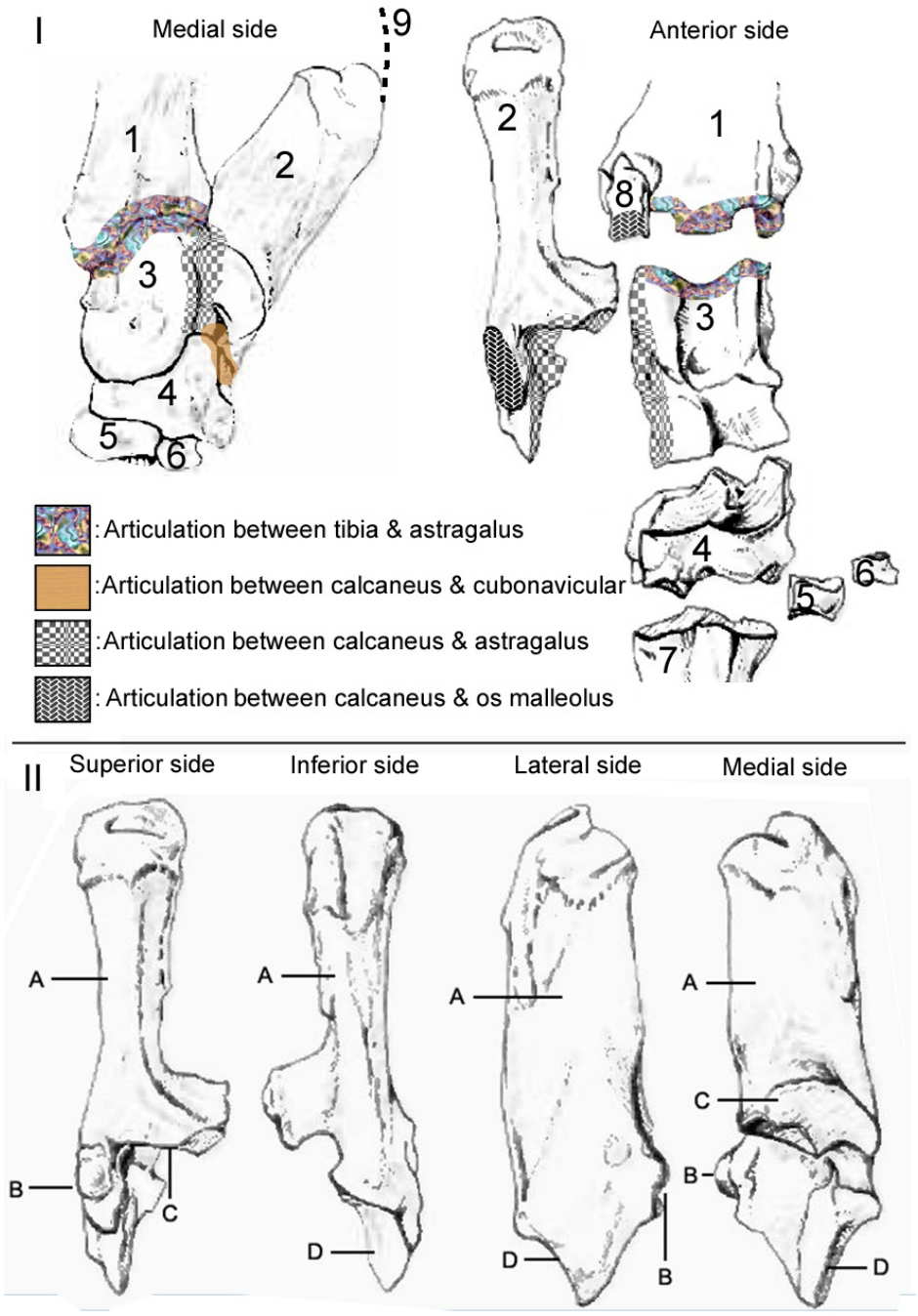


Figure 5.5: I=elements of the hock joint with indication of the articulations between the elements (1:tibia, 2:calcaneus, 3:astragalus, 4:cubonavicular, 5:Large cuneiform bone, 6:Small cuneiform bone, 7:metatarsus, 8:Os malleolus, 9:Insertion achilles tendon) II= parts of the calcaneus (A: tuber calcanei; B: articular surface to the malleolus; C: articular facet between calcaneus and astragalus; D: articular facet between calcaneus and cubonavicular) (adapted after Pales & Garcia 1981).

Most researchers (Alexander 1983, Polly 2007, 2008, Curran 2009, Warburton & Prideaux 2010, Galvez-Lopez & Casinos 2012) agree that the length of the lever arm of the calcaneus (the tuber) determines the force produced by the limbs as they push against the ground. Increasing the length of the calcaneus will increase power, but will make the joint move slower (Curran 2009, 2012). Similar to the phalanges, morphological variation in the calcaneus is explained in Curran's (2009, 2012) model by differences in predator evasion strategy between species of different environments. A shorter calcaneus will be less powerful, but allow for quicker movement (Curran 2009). Therefore, species that use bounding leaps to escape predators (mostly in closed habitats) are thought to have longer calcanei, while animals in open habitats are predicted to have shorter calcanei (Curran 2009).

In addition, the rest position of the calcaneus is also thought to differ between open habitat forms and closed habitat forms. If the calcaneus is positioned more vertically on the astragalus and the cubonavicular, the distance covered by the lever arm is shorter, but less powerful (Curran 2012), an observation also made for carnivores (Polly 2008). This morphological adaptation is associated with animals of open environments that increase their number of paces when accelerating (Gambardyan 1974, Geist 1998, Curran 2012). Cervids adapted to closed environments, on the other hand, have a calcaneus with a more horizontal neutral position. When the gastrocnemius muscle contracts more power is generated, which is especially advantageous in species that escape predators by series of bounding leaps (Curran 2009, 2012). In the osteomorphology of the calcaneus this is thought to be seen in a more oblique orientation of the articular surfaces on the anterior side in open habitat species (Curran 2012). Polly (2007) adds that in cursorial animals, the calcaneus is tightly locked to the astragalus to minimize movement to the parasagittal plane. As a result, the ridges and grooves on the articular surfaces between the calcaneus and astragalus are thought to have the highest relief in cursorial animals (Polly 2007). In some mammals the calcaneal articular facet

for the malleolus probably helps in stabilizing medio-lateral movement during locomotion (Scarborough et al. 2016).

Further considerations about functional morphology

Although Köhler (1993) reconstructed potential joint movements in the digits by testing maximal extension and flexion of the phalanges in osteological specimens, the above mentioned functional models (Leinders 1979, Köhler 1993) should ideally be tested in a more holistic, comparative approach that links ecology, performance and musculoskeletal anatomy. It is better to investigate functionally interconnected complexes of attributes together, to make sure that a more complete understanding of the individual attributes (i.e. osteomorphological traits) can be achieved (Bock 1994). Recent studies on muscle structure in ruminants, such as those by Curry *et al.* (2012) and Kohn (2014) can be instructive and have, for example, shown that differences in muscle type and oxidative capacity between bovids with different ecological affinities, may be correlated with cursorial effectiveness and jumping ability. These studies unfortunately don't link their findings with morphological adaptations in the skeleton, but can be instructive for ecomorphological studies on artiodactyl skeletal elements.

As such, holistic studies are currently lacking; researchers so far have had to rely on more general ideas about the relationship between performance, morphology and ecology. Curran (2009, 2012, 2018) emphasized the importance of increased strength for obstacle jumping in animals adapted to closed environments, while Kappelman's (1988) femoral studies, in contrast, associated closed environment species with a higher need for maneuverability. Leinders (1979) argued that species of open and dry environments have a more developed capacity for horizontal jumping, zig-zag running and stotting. Weighing these statements against some of the available behavioural data on predator evasion strategies in free ranging artiodactyls (Caro 1986, 1994, Caro *et al*. 2004), some further conclusions can be drawn.

Tacking or zig-zag running is probably more common amongst bovids living in open habitats (Caro 2004) and bounding leaps are more likely to occur in bovids when the topography is more rugged or when vegetation is tall (Caro 1994). These observations are in accordance with Curran's model, associating species of closed environments with obstacle jumping (Curran 2009, 2012, 2018). However, they do not confirm Leinders' (1979) emphasis on horizontal leaps and stotting in animals adapted to open environments. It is correct that stotting does occur more frequently in open landscape forms, but it is probably an indirect way to avoid being chased and not a true locomotory adaptation to escape during flight (Caro 1994, 2004). Leaping is actually more likely to occur in closed environments (Caro 1994). The importance of zig-zag running as an adaptation in open environment species (Leinders 1979) is acknowledged.

Ecomorphological hypotheses

Building on the above observations, a number of hypotheses are formulated here about the morphology of the intermediate phalanx (Fig. 5.4) and the calcaneus (Fig. 5.5) with respect to habitat:

- The proximal articulation of the intermediate phalanx is predicted to be deeper or more concave in species adapted to more open/drier environments: Following Köhler (1993), this trait might be related to a reduction in medio-lateral movement in the proximal interphalangeal joint to avoid disarticulation in more cursorial taxa. Species adapted to wet environments are predicted to have a shallower proximal articular surface that allows for more medio-lateral movement on a less predictable substrate (i.e. splaying of the digits).
- The plateau postarticulaire of the intermediate phalanx is predicted to be shorter in species adapted to drier/more open environments: The shape of the plateau

postarticulaire is probably not related to splaying of the phalanges, as it does not influence medio-lateral movement. It does, however, potentially restrict movement in the sagittal plane. Therefore I follow Leinders (1979) and associate a reduced plateau postarticulaire as an adaptation to increase flexion in the sagittal plane which could result in a more effective "pogostick effect" and heightened capacity to withstand forces during sudden breaks when zig-zag running or when taking large (horizontal) jumps.

- The extensor process on the anterior side and the palmar extensions on the posterior side of the distal articular surface of the intermediate phalanx are predicted to be further extended in species adapted to more open/drier environments: This is probably related to increased flexibility of the terminal phalanx in the sagittal plane and may also amplify the "pogostick effect" and increase the capacity to withstand higher forces during sudden breaks when zig-zag running or when taking large (horizontal) jumps (Leinders 1979).
- The shape of the distal articular surface of the intermediate phalanx is predicted to be round on the medial and lateral side in species adapted to closed or wet environments and characterized by a posterior apex on the medial side in species adapted to open environments: This is probably related to the splaying of the phalanges (Köhler 1993), as a rounded, equal shape of the articular surface on the lateral and medial side of the distal articulation allows more medio-lateral movement than an unequally shaped, medially pointed distal articular surface.
- The general shape of the intermediate phalanx is predicted to be more gracile/robust in species adapted to wet/closed or open/dry environments: Köhler (1993) associated species adapted to open/dry environments with more gracile phalanges. Contrarily, Degusta and Vrba (2005a, 2005b) linked gracile phalanges with species adapted to wet

substrate. Although none of these authors gave a true functional explanation to these differences it will nevertheless be informative to test whether gracility in the intermediate phalanx is in any way correlated with environmental differences.

- The relative length of the tuber calcanei is predicted to be greater in species adapted to closed environments and shorter in species adapted to open environments: A longer tuber calcanei increases the lever arm and provide more powerful, but slower movement of the lower hind leg. This morphotype is associated with animals that escape predators using bounding leaps. A shorter tuber calcanei and thus shorter lever arm provides less strength, but quicker movement. This is linked with animals that rely on speed to evade predators (Curran 2009, 2012).
- The articular surface supporting the malleolus is predicted to be larger in species adapted to open environments. An increase in relative size of this articular surface might provide more stability in the ankle joint (Scarbourough *et al.* 2016), an adaptation that might be associated with more cursorial species of open environments.
- A more oblique orientation of the articular facets between calcaneus and cubonavicular and between calcaneus and astragalus is predicted for species adapted to more open environments. Calcanei with a more vertically positioned tuber calcanei are able to generate less power, but a higher pace during contraction. This is associated with animals living in open environments that primarily rely on speed to escape predators (Curran 2009, 2012).

5.3 Geometric Morphometrics

One of the advantages of the ecomorphological method is that the morphology of skeletal elements can be quantified and objectively compared (Andrews & Hixson 2014). But how morphology is quantified has an important effect on what kind of data is captured in a

morphometric dataset (e.g. Evin *et al.* 2013a, Gruwier *et al.* 2015). Ecomorphological studies of artiodactyls have traditionally used linear measurements by means of calipers to quantify osteomorphological traits (e.g. Kappelman 1988, Bishop *et al*. 1996, Scott 2004, Weinand 2005, Kovarovic & Andrews 2007, Plummer *et al*. 2008), but a number of recent studies (e.g. Cucchi *et al.* 2009, 2011, Evin *et al.* 2013a, 2013b, Brophy *et al.* 2014, Forrest *et al*. 2018) have pointed out that Geometric Morphometrics, or GMM, can be used as an alternative way to effectively quantify artiodactyl morphology.

Generally speaking a morphometric study aims to report morphological variations within a collection of specimens by means of quantitative descriptions of aspects of morphology, resulting in abstract representations of the studied objects (O'Higgins 2000). Geometric morphometrics shares this goal with linear morphometric approaches and should be seen as a further development in this field that has come of age in the last few decades (e.g. Bookstein 1991, Rohlf & Marcus 1993, Rohlf 1998, Klingenberg 1996, O'Higgins 2000). As such, GMM can be described as a set of methods that analyzes the relative positions of anatomical landmarks and sets of points used to approximate curves and surfaces to quantify size and shape (Jensen 2003, Viscosi & Cardini 2011). Shape is defined here as all geometric information after location, scale and rotational effects are filtered out from the object (Kendall 1977, Zelditch *et al.* 2004). It encompasses methods and techniques of data acquisition and analysis, the results of which can be mapped in shape space and used to visualize shape variance within and between groups of specimens (Slice 2005, Plomp 2013).

In practice GMM is generally founded on the use of landmark data, where a landmark is a precisely defined point on a biological structure, the position of which is recorded by Cartesian coordinates (Baab *et al.* 2012). The definition of these landmarks is based on criteria of homology of the structures one wishes to quantify (Baab *et al.* 2012). In other

words, landmarks should be anatomical loci that do not alter their topographical positions relative to other landmarks, that provide enough coverage of the structure, and that can be easily identified (Zelditch *et al.* 2004). How and where landmarks are placed depends on the research questions being asked. Questions related to functional aspects of form may require a different placement of landmarks than questions related to aspects of evolution or ontogeny (Viscosi & Cardini 2011). In any case, the choice or selection of landmarks is an important step in any morphometric analysis (Viscosi & Cardini 2011).

Landmarks used in GMM can be divided into different types. Type I landmarks are characterized by having the strongest homology and are defined as locations where multiple discrete tissues intersect (Bookstein 1991, Baab 2012). Type II landmarks have no real biological correspondence, but their homology is supported by the surrounding structures (Bookstein 1991, Baab 2012). Type III landmarks are extreme points only defined by some distant structure (Bookstein 1991, Slice 2005). In a fourth type, called semilandmarks, the anatomical loci are not homologous by themselves. Only the wider structure or surface where these landmarks are positioned is homologous (Baab *et al.* 2012). Landmarks can be defined in two or three dimensions. In cases where landmarks are registered in 3D, they are defined by three (x, y and z) instead of two (x and y) Cartesian coordinates (Zelditch *et al*. 2004).

Although linear morphometrics still hold an important place in palaeontological and biological analyses (Killick 2012), GMM has a number of advantages over standard linear approaches. A first advantage is that the geometry of a measured object is retained in the data (Slice 2005). Contrary to linear morphometrics, measurements in GMM are not independent and can preserve both the dimensions of the object as well as the spatial relationships among the dimensions (Rohlf *et al.* 1993, Zelditch *et al*. 2004, Baab *et al.* 2012) (Fig. 5.6). Using ratios of variables can partially resolve these issues in linear morphometrics (e.g. Scott 2004,

Albarella 2009), but such an approach has limitations when it comes to quantifying multifaceted anatomic structures such as skeletal elements (Baab *et al*. 2012). GMM has the advantage that it is capable of quantifying more complex and subtle morphological differences (Strand Vidarsdottir *et al*.2002, Perez *et al*. 2007).

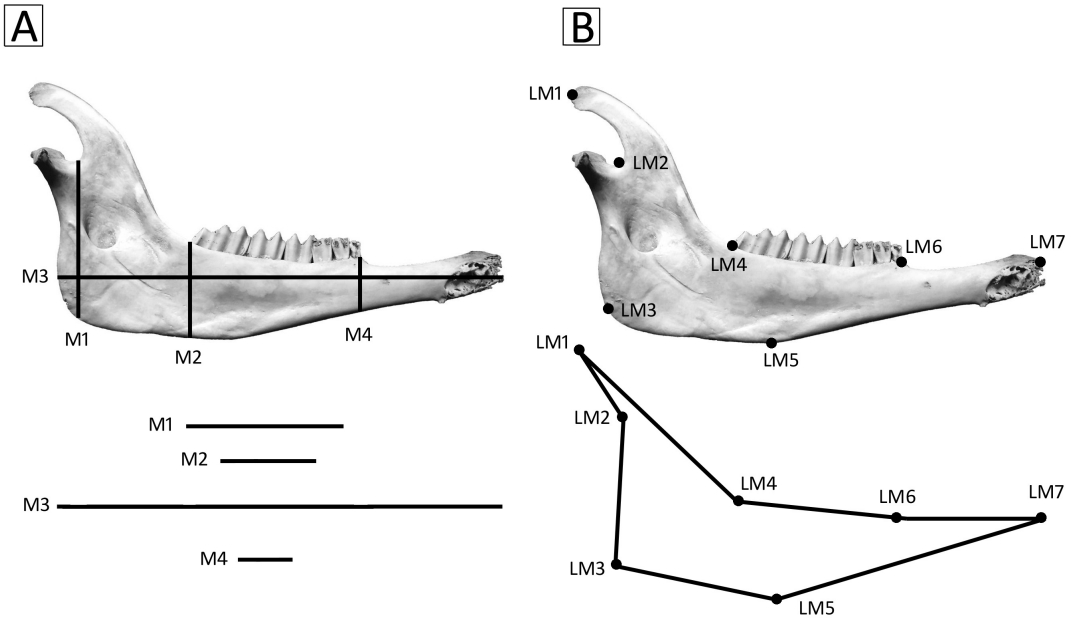


Figure 5.6: Hypothetical linear measurements (A) and GMM landmarks (B) on an artiodactyl mandible illustrate differences in retained data between the two methods. Method 'A' results in a set of independent dimensions. Method 'B' results in several Cartesian coordinates that preserve dimensions and spatial relationships. (M=measurement, LM=landmark). Photo adapted from Fischer 2014.

A second problem that GMM provides an answer to, is that in linear morphometric studies size forms a significant component of measurements (Zelditch *et al.* 2004). Although size sometimes is an essential part of palaeoecological studies, it is a confounding factor when one is specifically looking for morphological differences in osteological elements. While some techniques have been developed to control for body size in linear morphometrics (see section 4.3), GMM provides a more effective way to study morphology in isolation (Viscosi &

Cardini 2011). In practice this is usually done by performing a Generalized Procrustes Analysis (GPA) on the raw coordinate data, a process that removes information about size, orientation and location (Zelditch *et al.* 2004). In this process two or more configurations of landmarks are translated to a common location by superimposing their centroids, after which they are scaled to unit centroid size and rotated so that the distance between corresponding pairs of landmarks is minimized using a least-square algorithm (Zelditch *et al*. 2004, Baab 2012). The remaining difference between specimens corresponds to differences in shape (Bookstein 1991). GPA is one of a number of superimposition methods, but it is the most standard method used in GMM and has several advantages, such as high statistical power and increased accuracy in estimating sample means (Viscosi & Cardini 2011).

As a result of translation, rotation and scaling during the GPA analysis, landmark configurations lose degrees of freedom. The number of degrees of freedom lost can be calculated using the following equation: $pk-k-k(k-1)/2-1$, where p is the number of landmarks and k is the number of dimensions. For three dimensional analyses this translates to $3p-3-3-1$, or $3p-7$ (Slice 2005). In other words, GPA leads to a loss of seven degrees of freedom in three dimensional analyses (Slice 2005, Viscosi & Cardini 2011). The shape space that remains after rotation, translation and scaling is called Kendall's shape space (Kendall 1977). This shape space, however, describes shape in a curved, non Euclidean way (Slice 2001). This is problematic as most statistical methods require data to be in flat Euclidean space (Viscosi & Cardini 2011). This is solved by projecting the coordinate data into Euclidean space tangent to Kendall's shape space (Rohlf 1996, Owen 2013). This orthogonal projection from the Generalized Procrustes Superimposition preserves the distance between specimens in both shape spaces and does not result in any loss of shape information (Slice 2005). All further analysis can therefore be performed in this tangent Euclidean shape space.

It should be mentioned that although GPA scales landmark configurations to standard size, this does not exclude potential allometric size differences from the dataset (Zelditch *et al*. 2004). These have to be dealt with separately in further statistical analyses. Moreover, isometric size is still retained separately as an independent variable in the form of 'centroid size' (Zelditch *et al.* 2004). This commonly used measure of size in GMM is calculated as the square root of the sum of squared distances of each landmark in a landmark configuration to the configuration's centroid (Baab *et al*. 2012). It is a useful measurement of the overall scale of a landmark configuration (Strand Vidarsdottir *et al.* 2002, Plomp 2013) and can be included again in further statistical analysis whenever needed. Transformation to its natural logarithm is often used to scale centroid size to the mean configuration (Viscosi & Cardini 2011, Owen 2013).

A third advantage of GMM is that changes in morphology can be more clearly visualized and are quite easily produced (Zelditch *et al.* 2004).This is usually done by making use of transformation grids that describe changes in shape from one specimen to another as distortions in a grid (Zelditch *et al.* 2004). A commonly used visualization method used for landmark configurations is the thin plate spline interpolation technique (Bookstein 1991) (Fig. 5.7). This method provides a visually interpretable description of a deformation, using procrustes distance as a metric (Zelditch *et al.* 2004). It illustrates on a grid the amount of deformation that is needed to change a form from a reference shape such as the mean shape of a group (Zelditch *et al.* 2004, Plomp 2013).

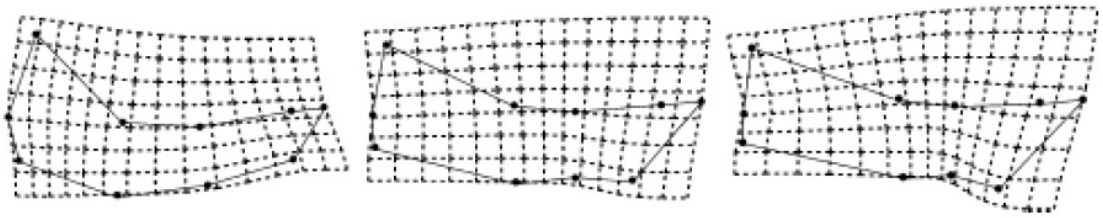


Figure 5.7: Thin plate spline deformation grids of a landmark configuration of a mammalian mandible illustrate shape changes in GMM. Figure adapted after Figueirido et al.2009.

5.4 Morphometric protocols and the application of GMM to the cervid limb

GMM has been increasingly applied in palaeoanthropology over the last decade and many studies have used these techniques directly on primate materials (e.g. Delson *et al.* 2001, Harvati & Weaver 2006, Baab 2008, Cardini & Elton 2011, 2017, San Milan *et al.* 2015). In addition, GMM has been used with variable intensity in morphometric studies of almost every other mammalian order (e.g. Bignon *et al.* 2005, Caumul & Polly 2005, Meloro 2007, 2008, Figueirido *et al.* 2009, Owen 2013) and for a number of purposes.

Although several recent GMM studies have focused on the Suidae (e.g. Cucchi *et al*. 2009, 2011, Ottoni *et al.* 2013, Owen 2013, Evin *et al.* 2013a, 2013b, Oueslati & Cronier 2014), these techniques are not yet commonly applied on fossil cervids and bovids. Some recent studies (Curran 2009, 2012, 2015, Brophy *et al.* 2014, Forrest 2017, Forrest *et al*. 2018) have nevertheless demonstrated that GMM is at least equally suitable for morphometric studies in these families. According to Forrest (2017), bovid ecomorphological studies based on 3D GMM have higher classification success rates when using LDA models (see section 5.5 for explanation), than studies based on linear measurements. Curran (2009, 2012, 2015), using 3D GMM specifically on cervid bones, also achieved high classification success rates in her analyses. Brophy and colleagues (2014) made use of a two dimensional GMM model, applied

on photos of bovid teeth, based on the assumption that the flat occlusal surface can be easily quantified in a 2D projection. Although the appropriateness of using either a three dimensional or two dimensional model should ultimately be dictated by the research questions and the nature of the anatomical structure that is digitized (Buser *et al.* 2018), it seems clear from the above mentioned studies that GMM is suitable for the quantification of cervid osteomorphology.

This study is concerned with the ecomorphology of two complex anatomical elements of the lower hindlimb: the calcaneus and intermediate phalanx. It was therefore considered appropriate to make use of a three dimensional model and thus 3D coordinate data were collected at a number of anatomical loci on the two elements. For this purpose raw data in the form of 3D surface scans were generated using a NextEngine laser scanner (model 2020i): a portable three dimensional surface scanner able to capture 3D data by projecting a laser beam on an object placed on a rotating platform. Using a support pole, the object is stabilized during rotation and scanned from different angles. From the resulting distance measurements, a 3D object was generated in the associated software package 'Scanstudio HD v. 1.3.2'. Individual scan divisions were manually cleaned and aligned into a fused 3D-object and saved in .ply format. Scan settings were set at 360°, eight divisions, high definition (2000 points/in^2) and at wide range.

To virtually place the landmarks on the 3D-objects, the resulting .ply-files were uploaded in Landmark editor 3.0, a software package developed to easily place landmark points accurately and with high repeatability on complex surfaces (Wiley *et al.* 2005). In this software six landmarks were placed on the calcaneus and eight landmarks on the intermediate phalanx. A limited number of landmarks were used for each element because Geometric Morphometric data results in high numbers of variables. Although there is no reliable rule of thumb for an

exact sample size/number of variables ratio (*N*:*p*) (Maccallum & Widaman 1999), it is generally advised for further statistical analysis to avoid low *N*:*p* ratios (see e.g. Cattell 1978, Gorsuch 1983, Evin *et al.* 2013a). As palaeontological datasets, including this one, are often limited in size, I chose to develop models with a relatively small number of variables to maximize the accuracy of group estimation and minimize the probability of errors.

As this dissertation deals with the ecological and functional morphology of two different and distinctive anatomical elements, a unique set of landmarks to capture shape information was developed for each element. All landmarks used in the two models were either type I or type II landmarks, because they have the most biological relevance (Zelditch *et al.* 2004). The locations were chosen because of their relevance to the functional hypotheses and because they were considered to represent the shape of the elements as a whole. They were also inspired by earlier ecomorphological models developed for the same elements in artiodactyls (Degusta & Vrba 2005a, 2005b, Kovarovic & Andrews 2007, Curran 2009, 2012, 2015).

On the calcaneus, the first landmark (LM1) was located on the most posterior point of the tuber calcanei (Fig. 5.8). Landmark 2 (LM2) was located on the most anterior point of the cubonaviculair articular surface. Landmark 3 (LM3) was located on the most posterior point of articular surface supporting the os malleolus and landmark 4 (LM4) on the most anterior point of the os malleolus articular surface. The fifth landmark (LM5) was located on the most superolateral point of the posterior astragalar articular surface. Landmark 6 (LM6) was located on the most inferolateral point of the posterior astragalar articular surface.

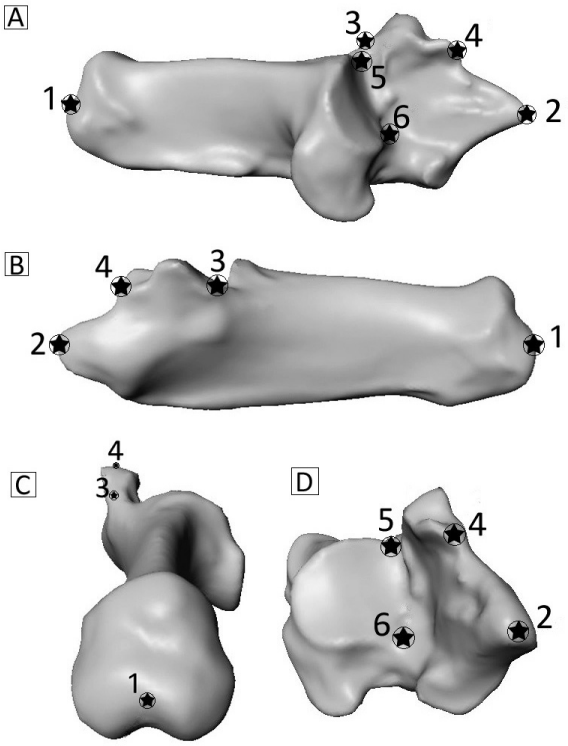


Figure 5.8: Landmarks 1 to 6 recorded on a 3D model of a calcaneus. A= medial view, B= lateral view, C= posterior view, D=anterior view.

On the intermediate phalanx, landmark 1 (LM1) was located on the most anterior point of the proximal articular surface (Fig. 5.9). Landmark 2 (LM2) was found on the most proximal point of the anterior extensor process. The third landmark (LM3) was located on the most posterior point of the distal articular surface at the junction between the left and the right facet of the articular surface, respectively supporting the medial and lateral portion of the distal articulation of the proximal phalanx. Landmarks 4 (LM4) and 5 (LM5) were found on the most posterior point of the lateral and medial extensions on the posterior side of the plateau postarticulaire respectively. Landmark 6 (LM6) and 7 (LM7) were located on the most proximal points of the medial and lateral palmar extensions on the posterior side of the phalanx. The eighth landmark (LM8) is positioned on the apex and most distal point of the medial ridge of the distal articular surface.

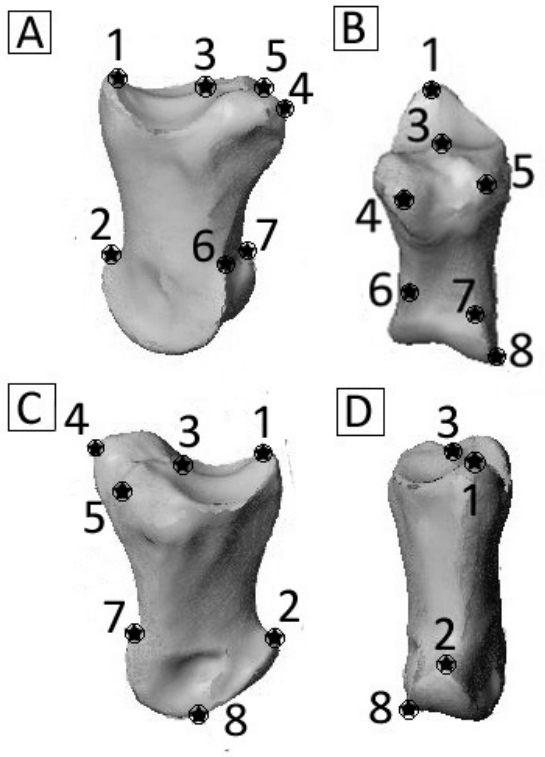


Figure 5.9: Landmarks 1 to 8 recorded on a 3D model of an intermediate phalanx. A= lateral view, B= posterior view, C= medial view, D=anterior view.

The resulting coordinate data for each specimen were then exported from Landmark editor in .PTS format and manually converted and appended into .TPS format. The appended file was then uploaded in Morphologika 2.5, an integrated morphemetrics package that is used for examining shape and size variation in objects described by landmark configurations (O'Higgins & Jones 2006). Morphologika was used to perform a Generalized Procrustes Analysis on the dataset in order to remove information about size, orientation and location from the coordinate data. From the output-file generated by the software, (log)centroid size was also saved for each specimen. Although Morphologika was not used for further statistical analysis of the morphometric data, a PCA was performed in this software on the mean shape calculated for each habitat/functional group, as a method (A. Cardini pers. comm.) to generate

thin plate spline visualizations of shape changes along each between groups principal component axis (see section 5.5).

The data matrices with procrustes residuals were exported from Morphologika and ordered by habitat/functional group or taxonomic group and imported in PAST 2.17 (Hammer *et al.* 2001) for further statistical analysis. This statistics package was especially designed for numerical analysis in palaeontology (Hammer *et al*. 2001) and allows for most multivariate analyses needed in GMM studies.

This procedure was initially performed for each anatomical element on a dataset with all extant specimens. The (procrustes fitted) data generated during this first analysis was used for the ecomorphological model based on extant cervid species. For the analyses of the palaeontological materials the procedure was repeated: newly appended .TPS files, with extant specimen data and a selection of fossil specimens included were created, and a new GPA analysis was performed on each individual dataset.

5.5 Statistical analysis

To investigate potential habitat prediction based on cervid hindlimb elements, a number of statistical analyses were conducted on the morphometric data. Most ecomorphological studies primarily make use of ordination methods such as Canonical Variates Analysis (e.g. Scott 2004, Curran 2009, 2012, 2015) and Principal Components Analysis (e.g. Bignon *et al*. 2005, Figueirido *et al.* 2009, Forrest *et al.* 2018) that are used to simplify descriptions of variation between specimens or groups (Zelditch *et al.* 2004).

In this case Principal Components Analysis (PCA) was chosen as the main analysis to explore morphological variation in the dataset. PCA is a multivariate statistical technique that simplifies patterns of variation and makes interpretation easier by transforming variables into

new artificial ones called principal components (PC's). This is done by rigidly rotating the original data into new linear re-combinations (Dryden & Mardia 1998, Zelditch *et al.* 2004). Principal components are orthonormal eigenvectors of the covariance matrix and can be considered independent and further analyzed accordingly (Dryden & Mardia 1998). Conducting a PCA on shape data does not lead to changes in spatial relationships between specimens. The original structure of the data remains unchanged as only the axes on which the data is projected are rotated (Viscosi & Cardini 2011). A good analogy is to compare specimens in a PCA with a cloud of points in multidimensional space, where only the point of view of the observer is changed to a better position to get a view on the longest sides of the cloud (Viscosi & Cardini 2011).

In PCA, the first component describes the largest part of the variance in the dataset. Each following PC describes the next greatest part of the variance (Owen 2013). This means that most of the variation in a sample is usually described by the first few PC's (Zelditch *et al*. 2004). As such, PCA can be used as a dimensionality reduction method. This is especially useful in the case of 3D GMM coordinate data that usually consists of particularly high numbers of variables. Using a Principal Components Analysis therefore simplifies interpretation and clarifies what has to be explained (Zelditch *et al.* 2004).

In many ecomorphological studies Linear Discriminant Analysis (LDA) is the preferred statistical analysis (e.g. Kappelman 1988, Plummer & Bishop 1994, Plummer *et al.* 2008, Degusta & Vrba 2003, 2005a, Kovarovic & Andrews 2007, Forrest 2017). This ordination method functions in a similar way as PCA in that it constructs a new coordinate system from linear re-combinations of original variables (Zelditch *et al.* 2004). However, LDA is used to describe differences among group means, whereas PCA is primarily used to describe differences among specimens (Zelditch *et al*. 2004). The disadvantage of LDA is that it uses *a*

priori assigned groups and looks for the direction of greatest variance between these groups by distorting shape space to minimize within-group variance (Klingenberg & Monteiro 2005, Seetah *et al.* 2012). This can potentially lead to overly optimistic group separation or over-fitting of the data (Kovarovic *et al*. 2011, Seetah *et al*. 2012).There are a number of factors that influence the chances of over-fitting. To avoid an over-fitted model, LDA typically requires equality of within-group covariance matrices, sufficiently large total sample size and group sample sizes and limited group inequality (Kovarovic *et al.* 2011). These assumptions are often violated in archaeological and palaeontological datasets and are sometimes hard to test (Kovarovic *et al.* 2011). As the datasets (especially the palaeontological ones) used in this dissertation are relatively small and of unequal size we followed Seetah and colleagues (2012) and instead of LDA, used a between groups Principal Component Analysis (bg-PCA) to explore between group morphological variation. In this approach eigenvectors are derived from the variance-covariance matrix of the group means instead of all the data-points, after which the individual specimens are projected onto them (Seetah *et al*. 2012). In other words, the bg-PCA will look for the axes of greatest variance between the groups mean shapes instead of that of all the specimens. This approach has the advantage that it is more robust to over-fitting and still preserves the original procrustes distances in shape space, but at the same time emphasizes between group differences (Seetah *et al*.2012).

In this dissertation all Principal Components Analyses (except when explicitly stated) were based on variance-covariance matrices of group means. In the first place, analyses were run on the procrustes residuals of a dataset of only extant specimens. For the analysis of the palaeontological specimens, PCA's were separately run on a combination of all extant specimens and a number of selections of fossil specimens. All PCA's were conducted in PAST 2.17.

Clusters in scatter plots resulting from ordination methods such as PCA are valuable for interpretation, but do not necessarily represent statistically distinct entities (Zelditch *et al*. 2004). Therefore additional statistical methods are needed to further determine statistical significance between designated groups (Zelditch *et al*. 2004, Goodpaster & Kennedy 2011). There is currently no standard metric that has been widely adopted to assess the statistical significance of cluster separation in PCA scatter plots (Goodpaster & Kennedy 2011). In this case an approach was taken, following work by Polly (see Schutz *et al.* 2009, Polly *et al*. 2013b), that involved conducting a MANOVA (Multivariate Analysis of Variance) on the relevant Principal Component scores. However, standard parametric statistical analyses, such as MANOVA, require that certain assumptions are met such as variance-covariance matrices that are homogeneous across groups and normal distribution (Lopez-Lazaro *et al*. 2018). This is not necessarily the case for GMM datasets and especially multivariate normality can be difficult to test in highly dimensional data resulting from 3D GMM (Cardini *et al*. 2015). To avoid violating these assumptions a non-parametric MANOVA (NPMANOVA), where significance was obtained from permutations (Anderson 2001), was used to test for differences between groups in multidimensional space. Non-parametric MANOVA tests were run on a data matrix including all relevant (i.e. describing a sufficient amount of the total variance) principal component scores. In cases where between-group differences were significant, the overall NPMANOVA was followed by a post-hoc test in the form of pairwise NPMANOVAs between all pairs of groups, to asses which groups differed significantly.

The number of relevant components retained for further analysis was first assessed using the broken stick method (Frontier 1976). In this model it is assumed that if the total sum of the variance is divided randomly amongst the principal components, the distribution of the eigenvalues is expected to follow a broken stick distribution (Jackson 1993). Eigenvalues are thought to be relevant if they exceed the values generated by the broken stick model (Frontier

1976, Jackson 1993). Although there are several other methods to assess the number of principal components to retain (see Jackson 1993 and references therein), the broken stick method is considered to provide a good evaluation of the dimensionality relative to most other methods (Jackson 1993). In cases where the number of components to retain, as suggested by the broken stick model, was extremely low (e.g. only PC1), I followed the rule of thumb to retain a number of components that cumulatively accounted for at least 90% of the variance (Rea & Rea 2016). In addition to providing a measure for the number of PCs to extract for the NPMANOVA, the same components considered relevant by the broken stick method were also used for visual assessment of the PCA scatter plots and for the further analyses described in this section (ordinary least squares regressions, PGLS regressions, Kruskal-Wallis tests).

Next to the NPMANOVA, which was used to assess significance of group differences in multidimensional space, a univariate equivalent was used to assess statistical significance between pre-assigned groups on individual PCA axes (Bratchell 1989, Harvati 2004, Carrera *et al.* 2007). Here the non-parametric Kruskal-Wallis test was used (Zar 1996, Yao et *al*. 2013). This test compares the medians of multiple groups and can be considered a multi-group extension of the Mann-Whitney test (Zar 1996). In cases where the Kruskal-Wallis test resulted in significant differences between group medians, Mann-Whitney pairwise comparisons were conducted as a post-hoc test to assess which pairs of groups differed significantly.

It was explained in section 5.3 that Geometric Morphometrics provides a capable set of tools to study size and shape separately in a morphometric dataset (Zelditch *et al.* 2004). By using techniques such as Generalized Procrustes Analysis, the effects of isometric size differences can be excluded from a set of landmark configurations (Zelditch *et al.* 2004, Baab *et al*. 2012). Allometric size differences are, nevertheless, not excluded by the GPA procedure. To

account for allometric effects, potential correlations between size and shape were explored by regressing PC-scores against the natural log of centroid size, a method commonly used in GMM studies (e.g. Cucchi *et al.* 2011, Killick 2012, Owen 2013). Ordinary least squares regression is a technique that estimates the relationship between a dependent variable and one or more independent variables, to predict how the dependent variable behaves for a given value of the independent variable (Legendre & Legendre 1998). When significant correlations between size and shape are found in the regressions, they are considered as indicative of an allometric effect (Zelditch *et al.* 2004). Where allometry drives morphological differences, this was taken into account during interpretation of the results, but no attempt is made here to remove these allometric effects.

Statistical methods are often applied to the problem of phylogenetic non-independence (see section 4.3). In this dissertation phylogenetic generalized least squares (PGLS) regressions (Martins & Hansen 1997) were conducted on the relevant PC scores (as indicated by the broken stick model) to assess morphometric datasets for phylogenetic signals. PGLS works as a weighted regression analysis where data is weighted in accordance with the phylogenetic closeness of species (Price 2015). In other words, this generalized linear model incorporates phylogeny as an error term into the regression models of shape variables on habitat/locomotion (Martins & Hansen 1997, Rohlf 2001, Walmsley *et al.* 2012). Phylogenetic tree branch lengths are used to estimate phylogenetic covariance (Monteiro 2013). The covariance for two given species is proportional to the sum of branch lengths from the root to the last common ancestor (Monteiro 2013). It is assumed here that cervid traits evolved according to a simple Brownian motion model (Monteiro 2013, Barr & Scott 2014), where changes are random and independent from previous and subsequent changes (Felsenstein 1985, Barr & Scott 2014). Pagel's λ was used in this analysis as a measure for phylogenetic dependence (Pagel 1999). If values were close to 0, this indicated a low

phylogenetic signal and that the trait evolved independently of phylogeny. If values were close to 1, the phylogenetic signal was high and closely related species were more similar in morphology under a Brownian motion model (Molina-Venegas & Rodriguez 2017).

In this dissertation a modified approach was used, based on earlier methods developed for carnivore elements (Meloro *et al.* 2008, Walmsley *et al*. 2012), using the caper package (1.0) in R (Orme *et al.* 2018). Habitat/locomotion groups were transformed into dummy variables and regressed against the mean shape coordinates for each species. Phylogentic tree distances, included as error terms, were downloaded from the 10KTrees project website (Arnold *et al*. 2010) (Fig. 5.10). Although a discussion of the extant cervid species used in this dissertation is provided further down in section 5.8.1, it should be mentioned here that two of the species included in the main ecomorphological analyses (*Cervus* (*Rusa*) *marianna* and *Cervus* (*Rusa*) *alfredi*), were excluded from the PGLS regressions, as they were not part of the 10KTrees phylogenetic tree. In addition, two forms that were treated as full species in the main ecomorphological analyses (*Cervus elaphus* and *Cervus canadensis*) (see section 5.8.1), were in the phylogenetic tree considered conspecific and consequently lumped together in the PGLS regressions.

In addition, to study how phylogeny drove the behaviour of species in morphospace, the mean shapes per species were calculated and projected on the PCA scatterplots derived from the variance-covariance matrix of the habitat/locomotion group means. Minimal spanning trees were calculated to estimate the minimal total lengths connecting all datapoints as a visual aid in grouping together taxa (Hammer *et al*. 2001). If species clustered close together by specific, generic or tribal association, this was interpreted as an indication that the morphology was correlated with phylogeny (Curran 2015).

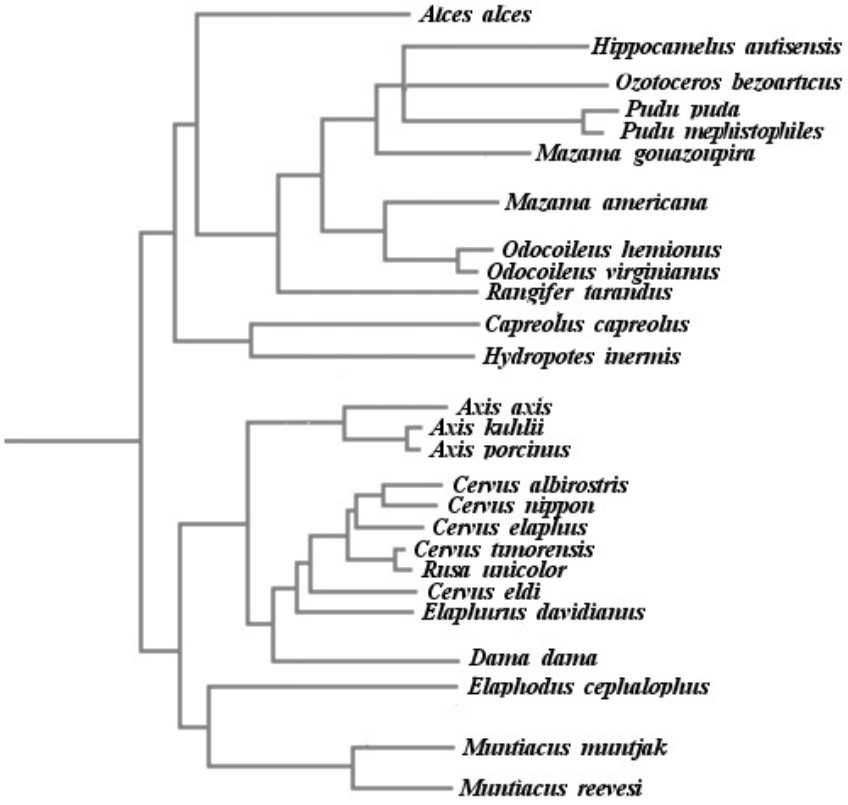


Figure 5.10: Phylogenetic tree of species used in this dissertation for PGLS regressions. Adapted from 10Ktrees (Arnold et al. 2010).

In most ecomorphological studies focused on artiodactyl phalanges (Degusta & Vrba 2005a, 2005b, Kovarovic & Andrews 2007, Curran 2009, 2012, 2015), no distinction is made between anterior and posterior phalanges because their position is often difficult to ascertain in fossil specimens. Although the ecomorphological model developed for the intermediate phalanx in this dissertation was based on posterior phalanges, fossil anterior and posterior specimens were combined in all further analyses. To test the validity of the assumption that the anatomical position (forelimb or hindlimb) of the phalanges does not significantly interfere with ecomorphological (and phylogenetic) signals, an additional test was conducted. A dataset composed of 16 intermediate phalanges (eight anterior and eight posterior) belonging to *Capreolus capreolus* and 10 intermediate phalanges (5 anterior and 5 posterior)

belonging to *Dama dama*, was submitted to a (between groups) PCA. Statistical significance between groups was tested using an NPMANOVA on the first four principal components.

Finally, many species of deer have marked sexual dimorphism (Geist 1998). This is most obvious in the presence of antlers in the males. Only in reindeer (*Rangifer tarandus*) both sexes possess such defensive weapons (Geist 1998). Although determining sex in post-cranial fossils of deer is difficult, sexual dimorphism can influence bone morphology in this region as well (Curran 2009). Most ecomorphological studies (e.g. Plummer & Bishop 1994, Kovarovic & Andrews 2007, Schellhorn 2009) have not explicitly tested for the confounding effects of sex differences. Moreover, the extant datasets used in this dissertation are also unsuitable for such tests as they lack sufficiently large samples of individual species of known sex. Although Curran's (2009) work on cervid post-cranials already indicated that the effect of sexual dimorphism is relatively small on the calcaneus and phalanges, a limited exploratory analysis was conducted on the *Dama dama* specimens used in this dissertation. Thus two separate analyses (one on the intermediate phalanx and one on the calcaneus), emphasizing male-female differences, were conducted on a dataset that consisted of only this species. To examine if specimens could be assigned to different sexes a (standard) PCA was performed on the two datasets, including respectively 10 intermediate phalanges and 10 calcanei. Significance of group differences was tested using an NPMANOVA on the first four principal components.

5.6 Error testing

To assess intra-observer error and the repeatability of the digitization protocol an adjusted version of the protocol developed by Adriaens (2007) was used. Five specimens of the calcaneus and the intermediate phalanx were randomly selected and scanned using the NextEngine and landmarked five separate times using the standardized landmarking

procedure. After procrustes superimposition, a standard PCA, based on the variance-covariance matrix of all specimens, was conducted on the dataset of the replicates. When the replicated specimens clustered tightly together on the first two axes of the PCA, the error due to differences in scanning/digitisation quality was considered low (Adriaens 2007). The following calcanei specimens were selected for error testing of the digitization process: KBIN 1290e (*Rangifer tarandus*), KBIN 1290g (*Rangifer tarandus*), CAR dd001 (*Dama dama*), KBIN 1297e (*Axis axis*) and KBIN 1297y (*Axis porcinus*). For the intermediate phalanx the following specimens were selected for error testing: MNHN 1879222 (*Cervus unicolor*), MNHN 129744 (*Cervus timorensis*), KBIN 2256 (*Dama dama*), MNHN nonr001 (*Hydropotes inermis*) and KBIN 3720 (*Axis axis*). See Appendix B for further details about these specimens.

Intra-observer error was tested using the same protocol, but only repeating the landmarking procedure and not rescanning the specimens. The landmarking procedure was repeated four times for another five specimens with three month intervals. The test was conducted four times on the same specimens held at the zooarchaeology labs of the University of Lille and the Center for Artefact Research (see Appendix B). For the intermediate phalanx these were the following specimens: CAR b056 (*Capreolus capreolus*), CAR b057b (*Muntiacus reevesi*), ULILLE 782 (*Capreolus capreolus*), ULILLE DD001 (*Dama dama*), ULILLE CE001 (*Cervus elaphus*). For the calcaneus the following specimens were included in the test: ULILLE 782 (*Capreolus capreolus*), ULILLE CC002 (*Capreolus capreolus*), ULILLE DD001 (*Dama dama*), CAR b057b (*Muntiacus reevesi*), CAR DD001 (*Dama dama*).

5.7 Habitat/locomotor categories

Defining habitats presents a challenge for studies that are based on comparisons with modern environments (Kovarovic 2004). As has been explained in chapter 4, assigning extant

specimens to predefined categories is an oversimplification of ecological reality, but a necessary requirement for further statistical analysis in ecomorphological studies (Curran 2009). Consequently, a six category system, somewhat similar to that found in many bovid studies (e.g. Kappelman *et al*. 1997, Degusta & Vrba 2003, 2005, Kovarovic & Andrews 2007) was developed in this dissertation. However, unlike earlier studies, I was chose to assign species in the first place to functional/locomotor categories rather than ecological categories. This was done to emphasize the fact that different morphotypes are thought to primarily differ as a result of functional differences related to locomotor strategy (Barr 2014a, 2014b). Only in a second step are these functional differences linked to different habitats or vegetation types. Although in practice this difference in approach is mainly theoretical, in some cases it can have an effect on how certain taxa are assigned to specific categories. This is exemplified in animals primarily adapted to closed environments. Such forms generally tend to have a more saltatorial predator evasion strategy, but have in some instances developed alternative means to optimally use their environment when fleeing from predators. This is the case for very large and heavy species such as moose (*Alces alces*) that tend to step over obstacles in their environment instead of jumping over them (Geist 1998). In these cases species were in the first place assigned to a group based on their locomotor strategy.

In addition, room was left for separate categories for forms that had either a more cursorial or saltatorial strategy, but that were associated with very specific environmental conditions (i.e. swamp environments, mountainous environments and tundra environments). Unlike some previous studies (Kappelman 1988, Curran 2009) wet adapted species were placed in a separate category in this study. In addition, Kovarovic and Andrews (2007) were followed in placing mountain adapted species in a separate category, albeit not subdividing this category in high altitude species of light cover or heavy cover. An overview of extant taxa and their

habitat assignments is given in Table 5.1. A breakdown of the number of species and specimens per habitat/locomotor group can be found in Appendix A.

Species	**Locomotion/ habitat group**	**Justification**
Alces alces	Type 1	Range of woodland habitats; not too far from water (Bauer & Nygrén 1999), but fast, more cursorial (trotting) lomotor strategy (Geist 1998).
Axis axis	Type 1	Dry deciduous habitats with scrub are favoured (Eisenberg & Seidensticker 1976). Cursiorial locomotor strategy (Geist 1998).
Axis porcinus	Type 5	Wet grassland, often associated with floodplains (Bhowmik *et al*. 1999). Runs awkwardly with head low, but at reasonable speed (Blandford 1888).
Axis kuhlii	Type 2	Very versatile but found in hill forest rather than marsh grassland like hog deer (Blouch & Atmosoedirdjo 1987). Outrun by dogs, probably not cursorial (Geist 1998).
Capreolus capreolus	Type 3	Versatile, often found in deciduous, mixed or coniferous forests, moorland and pastures (Stubbe 1999). Certainly not cursorial (Geist 1998).
Cervus albirostris	Type 4	Found in grassland, shrubland and forest at high altitudes in the eastern Tibetan Plateau (Leslie 2010). Uses rocky terrain to escape, but speedy flight (Geist 1998).
Cervus canadensis	Type 1	Open country grazer and cursorialist (Geist 1998).
Cervus elaphus	Type 1	Originally open deciduous woodland species, but also upland moors, pastures and meadows (Koubek & Zima 1999). Cursorial escape behaviour (Geist 1998).
Cervus eldi	Type 5	Variety of wet, open and grass dominated habitats (Tordoff *et al.* 2005). Good runners (Geist 1998).
Cervus mariannus	Type 2	Adaptable, primary and secondary forest, but forages in grassland (Taylor 1934). Anti-predator strategies unclear (Geist 1998).
Cervus nippon	Type 2	Woodlands with dense understory, but also forages in open grassy areas (Smith and Xie 2008). Saltatorial runner (Geist 1998).
Cervus timorensis	Type 1	Although flexible, essentially a cursorial, tropical and subtropical grassland species (Medway 1977, Geist 1998).
Cervus unicolor	Type 3	Found in a wide variety of forest types (Schaller 1967). Species of moderate speed (Blandford 1888).
Cervus alfredi	Type 2	It was known to rely on dense forest for refuge , but versatile and also makes use of open habitats (Rabor 1977).
Dama dama	Type 1	Adaptable species that can survive in a range of habitats, often open woodland, shrubland and grassland (Apollonio *et al*. 1998). It has a body-plan similar to *Megaloceros*, the most cursorial deer ever to exist (Geist 1998) and reaches high speeds similar to that of cursorial species (Janis & Wilhelm 1993).
Elaphodus cephalopus	Type 4	High altitude forests, close to water (Ohtaishi & Gao 1990). Saltatorial escape strategist (Geist 1998).

Elaphurus davidianus	Type 5	Low-lying grasslands and reed beds, often in seasonally flooded areas such as the lower Yangtze River valley and coastal marshes (Hu & Jiang 2002). Low running speed (Geist 1998).
Hydropotes inermis	Type 5	Prefers coastal plains, salt marshes, and riparian areas (Zhang et al. 2006). Fast, but leaps to escape predators (Geist 1998).
Hippocamelus antisensis	Type 4	Grassland species living at altitudes between 2000 and 5000 m (Gazzolo & Barrio 2016). Cursorial escape behavior (Geist 1998).
Mazama americana	Type 3	Bodmer (1997) states this Amazonian species occurs in humid forest borders. Slow and more saltatorial (Geist 1998).
Mazama gouazoubira	Type 3	Humid to dry regions where there are areas of woody or brush cover (Cartes 1998). More cursorial than M. Americana (Geist 1998).
Muntiacus muntjak	Type 3	This animal preferes rainforests and monsoon forests (Ekwal et al. 2012). Places objects between itself and the predator by jumping and giving conflicting signals (Geist 1998).
Muntiacus reevesi	Type 3	Preference for temperate or (sub-) tropical primary forest (Chiang 2007). Places objects between itself and the predator by jumping and giving conflicting signals (Geist 1998).
Odocoileus virginianus	Type 2	Cursorial capacity, but on occasion saltatorial (Geist 1998). Occupies a variety of habitats from northern forests to shrubby savannas (Potapov et al. 2014).
Odocoileus hemionus	Type 4	Associated with thickets and rocky outcrops. Steep and rugged terrain with brushlike vegetation is preferred, but versatile (Olson 1992). Less speedy, not cursorial (Geist 1998).
Ozotoceros bezoarticus	Type 1	Found in the semi-arid grasslands (Merino & Semeniuk 2011). Unclear in terms of escape behavior, but probably cursorial to some extent.
Pudu mephistophiles	Type 4	Lives especially in high altitude mountain forests and humid grasslands above the treeline (Escamilo et al. 2010). Saltatorial species (Geist 1998).
Pudu puda	Type 3	The Southern pudu inhabits dense temperate forest (Hershkovitz 1982). Saltatorial species (Geist 1998).
Rangifer tarandus	Type 1/6*	Tundra, but adapted for melted snow (Baskin 1986), Cursorial escape behavior (Geist 1998).

Table 5.1: Habitat assignments per species in alphabetic order (:Rangifer tarandus was placed in a separate tundra-category [Type 6] for the analysis of the phalanges).*

Thus six locomotor/habitat groups (type 1 to type 6) were devised to which each extant species was assigned. In the first group (type 1) animals were included that have a cursorial escape strategy and tend to live in more open environments. It should nevertheless be remembered that cervids are less flexible in their habitat preferences than bovids and are not often found in truly open, coverless environments such as dry grasslands or steppe (Geist 1998). Therefore this category groups together taxa that are adapted to open woodland (e.g. *Cervus timorensis*) and the few species that are adapted to dry open plains (e.g. *Ozotoceros*

bezoarticus). Open woodland is defined here as an area of trees with an open canopy of 40% or less closure (Thomas & Packham 2007). Such landscapes often (but not always) have a dry and firm substrate and have comparatively few obstacles that an animal can place between itself and a predator when being chased. As a result such species are more adapted for high speed and endurance, enabling them to escape potential predators by outrunning them (Curran 2009). The capacity for splaying the phalanges is not thought to be particularly well developed in this group (Köhler 1993, Curran 2009).

Type 3 species are animals that primarily rely on a saltatorial escape strategy and tend to live in more closed environments. This group includes animals of a number of forest types ranging from closed woodland, over temperate seasonal forest (e.g. *Pudu puda*) to tropical evergreen rainforest (e.g. *Muntiacus muntjak*). These environments are often associated with a relatively soft or wet substrate and with a high number of obstacles that can be used by an animal to place between itself and a predator during flight. Such animals have lower endurance and speed and evade predators by leaping over obstacles and diving in the undergrowth to break visual contact with their pursuer as quickly as possible (Curran 2009). Splaying of the phalanges is more developed in this group as an adaptation to more yielding substrates (Köhler 1993, Curran 2009).

Type 2 species are intermediate between type 1 and type 3 species. They are usually generalists that can easily adapt to either open- or closed environments and are found in softer and harder substrates. As a result they are neither true cursorial species, nor true saltatorial specialists (e.g. *Cervus marianna*). They lack the high speed and endurance of cursorial species, but are not as flexible or as good at leaping as saltatorial species. Their evasion strategy is intermediate between the two other groups and their capacity for splaying the phalanges is not particularly well developed for either very firm or very soft substrates.

Type 4 species are species found at high altitude in mountainous environments and are generally thought to be more saltatorial in escape behaviour due to their proximity to steep terrain with rocky outcrops (Curran 2009). They are, nevertheless, not as well adapted to these environments as mountain bovids (Geist 1998) and even when found at high altitude, they often prefer relatively flat terrain (e.g. *Cervus albirostris*) (Flueck & Flueck 2017). As a result these species can also show high endurance and speed and may be cursorial to some extent. Their capacity for phalangeal splaying is thought to be high (Köhler 1993, Curran 2009).

Type 5 species are found in open wetlands and, similar to type 1 species, associated with a cursorial escape strategy. These environments mostly have soft substrate and typical habitats are swamps (e.g. *Blastoceros dichotomus*), wet grasslands (e.g. *Cervus eldii*), and saltmarshes (e.g. *Hydropotes inermis*). Even though these habitats often have few solid objects to put between prey and predator, they are often vegetated with tall grasses or reedbeds that provide cover (Curran 2009). As a result species of this type don't necessary have to rely as much on speed and endurance as true cursorial forms (type 1) and may show some morphological traits similar to type 2 species. Their phalanges are thought to have a relatively high capacity for splaying (Köhler 1993, Curran 2009).

A final group (type 6) was solely composed of reindeer (*Rangifer tarandus*). This species has a cursorial evasion strategy and is found in fairly open tundra environments (Geist 1998). Reindeer phalanges, however, are thought to be adapted to the particular conditions present in the tundra: alternating episodes of frozen soil and melting snow that require additional grip (Hildebrand 1985, Nieminen 1990). It was therefore felt that at least for the limb extremities it was more appropriate to place this species in its own group.

5.8. Materials

5.8.1 Extant specimens

Data on extant specimens were collected at a number of institutes: the Royal Belgian Institute of Natural Sciences (Brussels, Belgium), the National Museum of Natural History (Paris, France), the Naturalis Biodiversity Center (Leiden, The Netherlands), the Natural History Museum Rotterdam (The Netherlands), the National Museum of Natural History (Washington D.C., U.S.), the American Museum of Natural History (New York, U.S.), the Charles-de-Gaule Lille III University (Lille, France), the University of Liège (Belgium) and the Center for Artefact Research vzw (Mechelen, Belgium). In addition, 3D data from a small number of specimens was shared by the Max Planck Institute of Evolutionary Anthropology (Leipzig, Germany) (Niven *et al*. 2009) and the Virtual Zooarchaeology of the Arctic project (Idaho University, United States) (Maschner *et al.* 2011, Betts *et al.* 2011). In Appendix B the institutions are listed where the latter specimens are held.

In total 166 extant individuals were studied, resulting in a dataset of 142 intermediate phalanges and 125 calcanei. The composition of the dataset was to an extent a function of the availability of species at the different institutes visited. Although the extant sample was not as extensive as in certain earlier works (e.g. Kovarovic 2004), all reasonably available data was collected and sample sizes were in the same range as in a number of other ecomorphological studies on artiodactyls (e.g. Weinand 2005, Curran 2009, Schellhorn 2009). For certain taxa (e.g. *Cervus elaphus*), larger numbers of skeletons were available, but it was decided that for each species a maximum 16 specimens were scanned of each element, to prevent the dataset from becoming too skewed towards more common species. While the majority of the specimens came from wild caught animals, some zoo specimens were included as certain taxa were extremely rare in museum collections (see Appendix B). Although captivity is known to

affect morphology in certain mammals (O'Regan & Kitchener 2005) captive specimens were still considered useful additions to maximize the diversity and sample size of the dataset. The modern sample of cervids was comprised of 29 different species, belonging to 6 tribes. Each species was assigned a three digit code that was used throughout this dissertation (Table 5.2).

Both males and females were included in the sample, but except for an exploratory analysis of between-sex morphological variation, no specific distinction was made between sexes in the analysis of the data (see section 5.5). An attempt was made to sample specimens evenly across sexes, but since most museum collections are biased towards male trophy-hunted specimens (Curran 2009) this was impossible for all taxa. Only adult, non pathological, specimens were included. Skeletons were considered adult when all epiphyses were fused and all teeth were erupted. In cases where only isolated bones were present, it was deemed sufficient if the epiphyses of the individual specimens were fused. Cervids from all geographical areas were included as it was felt that a dataset of only (Southeast-) Asian species would be too restrictive in terms of taxonomic diversity. The sampled species come from a wide range of habitats in Europe, Asia, North- and South America (Table 5.2). A more detailed list of all specimens is given in Appendix B.

When possible, the medial phalanx from the left posterior leg was selected for data collection. In cases where this element was unavailable or inappropriate for scanning, the lateral phalanx of the same leg or the medial phalanx of the opposite leg was selected. When necessary, scanned specimens were virtually mirrored using Meshlab 2.0. When selecting calcanei for scanning, I systematically opted for the left calcaneus. Some right specimens were also mirrored using Meshlab, in cases where the preferred side was unavailable. Preference was given to specimens that included more detailed associated catalog data (especially pertaining to locality).

Tribe	Species	Code	N	Calc	Ph2	Geographic range
Cervini	*Axis axis*	AXA	13	11	10	India
	Axis (*Hyelaphus*) *kuhlii*	AXK	3	2	3	Java (Bawean)
	Axis (*Hyelaphus*) *porcinus*	AXP	5	4	5	South-and Southeast Asia
	Cervus (*Przewalskium*) *albirostris*	CEA	1	-	1	Tibet and China
	Cervus (*Elaphurus*) d*avidianus*	ELD	3	3	3	China
	Cervus (*Panolia*) *eldii*	CEL	5	2	4	South-and Southeast Asia
	Cervus (*Rusa*) *timorensis*	CET	5	2	5	Java
	Cervus (*Rusa*) *alfredi*	CAL	2	1	2	Philippines
	Cervus (*Rusa*) *marianna*	CEM	1	1	1	Philippines
	Cervus (*Rusa*) *unicolor*	CEU	6	3	6	South-and Southeast Asia
	Cervus canadensis	CCA	7	4	5	North America
	Cervus elaphus	CEE	12	10	9	Western Eurasia and North Africa
	Cervus nippon	CEN	2	2	2	East Asia
	Dama dama	DDA	11	11	11	Europe and Western Asia
Muntiacini	*Elaphodus cephalopus*	ELC	5	3	4	East Asia
	Muntiacus reevesi	MUR	3	3	3	East- and Southeast Asia
	Muntiacus muntjak	MUM	6	4	6	South-and Southeast Asia
Capreolini	*Capreolus capreolus*	CAC	20	16	16	Europe and Western Asia
	Hydropotes inermis	HYI	11	11	8	China
Rangiferini	*Rangifer tarandus*	RAT	15	12	14	Northern Eurasia and North America
Odocoileini	*Hippocamelus antisensis*	HIA	1	-	1	North-East of South America
	Mazama gouazoubira	MAG	1	-	1	North-West of South America
	Mazama americana	MAA	6	2	5	North of South America
	Odocoileus virginianus	ODV	3	3	3	North- and Central America
	Odocoileus hemionus	ODH	3	2	2	West of North America
	Ozotoceros bezoarticus	OZB	1	1	1	Central South America
	Pudu mephistophiles	PUM	3	2	2	North-West of South America
	Pudu puda	PUP	5	5	3	South-West of South America
Alceini	*Alces alces*	ALA	7	5	6	Northern Eurasia and North America

Table 5.2: Extant species used in the dataset, including species code (Code), geographic range, total sample of studied skeletons (N), number of calcanei (Calc) and number of intermediate phalanges (Ph2).

5.8.2 Fossil specimens

3D surface scans were taken of fossil specimens at the Naturalis Biodiversity Center (The Netherlands, Leiden), the Museum für Naturkunde Berlin (Germany) and the Geological Museum of Bandung (Indonesia). A substantial amount of fossils were available for observation, but ultimately a sample of 80 sufficiently preserved specimens was selected for further analysis (Table 5.3). Left and right calcanei were included, but right specimens were digitally mirrored in Meshlab 2.0 for inclusion in the model. Similarly, fossil phalanges were mirrored in Meshlab to match their laterality with that of the extant specimens used in the

training set. Due to the difficulty of distinguishing anterior and posterior intermediate phalanges, both were included in the model. Incomplete bones were not studied because they generally perform worse in ecomorphological studies than complete bones (Curran 2009) and because of their tendency to give misleading results, as the missing values often alter the specimen's position relative to the group centroid in multivariate space (Bishop 1994).

The fossils used in this dissertation were found at several Early to Middle Pleistocene sites from Java (Fig. 5.11). The majority of the material came from sites where *Homo erectus* was confirmed to have been present (Trinil, Sangiran and Kedung Brubus). A smaller number of fossils were included that were found in the Kendeng Hills in the proximity of these larger, well studied sites and have been considered part of the Kedung Brubus biostratigraphic unit (Bangle, Sembungan, Butak, Banuraja) (von Koenigswald 1933, Brongersma 1935, van Heekeren 1957, Aziz & de Vos 1999). In addition, a number (N=15) of Early to Middle Pleistocene specimens from East/Central Java were included that lacked precise locality data, but were still relevant as they belonged to species that were also found in Trinil, Kedung Brubus or Sangiran. As such they are still informative about the habitat preferences of these species. In Appendix C a list with detailed catalog data is provided for all fossil specimens.

Locality	Biostratigraphic unit	Age	N	Calc	Ph2
East/Central Java	-	Early/Middle Pleist.	15	7	8
Trinil	Trinil H.K.	0.9 Ma	43	28	15
Sangiran	Trinil H.K./Kedung Brubus	≤ 0.7-0.9 Ma	16	9	7
Kedung Brubus	Kedung Brubus	0.7-0.8 Ma	2	-	2
Butak	Kedung Brubus	0.7-0.8 Ma	1	-	1
Bangle	Kedung Brubus	0.7-0.8 Ma	1	1	-
Sembungan	Kedung Brubus	0.7-0.8 Ma	1	1	-
Banuraja	Kedung Brubus	0.7-0.8 Ma	1	1	-
Total:	-	-	80	47	33

Table 5.3: Fossil specimens used in dataset, including find locality, associated biostratigraphic unit, estimated age, total sample of studied fossils (N), number of calcanei (Calc) and number of intermediate phalanges (Ph2).

Figure 5.11: Map of Java with the location of the palaeontological and palaeoanthropological sites where the studied materials were found.

The largest sample of 43 specimens, came from Trinil H.K. (hauptknochenschicht= main fossiliferous layer), the *Homo erectus* type locality. This site, first excavated by Dubois in the late 19th century, was found near the village of Trinil on the banks of the Solo River (de Vos 2004). A large part of the material that was included in this study (N=28) comes from this early excavation and is now kept at the Naturalis Biodiversity Center in Leiden as part of the Southeast Asian palaeontological collections. In addition, a sample (N=15) of cervid fossils that came from the early 20th century German campaign at Trinil, led by Selenka and colleagues (1911), was also included in the dataset. The latter collection was studied at the Museum für Naturkunde of the Humbolt University in Berlin.

The main fossiliferous layer (H.K.) found at Trinil is composed of volcanic tephra of an Early to Middle Pleistocene age (Watanabe *et al.* 1985). It is dated around 0.9 Ma (van den Bergh *et al.* 2001). The only cervids that were positively identified at this site are a rare muntjac (*Muntiacus kendengensis*) and the extinct, but commonly found, *Axis lydekkeri* (von Koenigswald 1933, van den Bergh *et al.* 2001, Gruwier *et al*. 2015). The larger deer, regularly found in younger sites on Java are absent from Trinil. Although there are indications that the limited number of species identified at Trinil are a true reflection of the taxonomic diversity

of the site (Gruwier *et al.* 2015), it can nevertheless not be excluded that some cryptid species were present in the unidentified (or identified) sample from Trinil. It is in this case *a priori* assumed that all specimens from Trinil, included in the dataset, belonged to *Axis lydekkeri*.

From the hominin site of Kedung Brubus only two fossils were appropriate for inclusion in the dataset. This second *Homo erectus* site was found in the southern part of the Kendeng Hills near the village of Kedung Brubus (Sondaar 1994) and is mainly composed of fluviatile deposits of sand, sandstone and pebbles (Watanabe *et al*. 1985). According to van den Bergh et al. (2001) the deposits represent a single faunal unit and can be dated between 0.7 and 0.8 Ma. The two studied specimens are thought to belong to the large sized *Cervus kendengensis*. Although no other specimens useful to this analysis were available from the site, the smaller *Axis lydekkeri* is also represented within this assemblage (van den Bergh *et al.* 2001, Gruwier *et al.* 2015). The materials from Kedung Brubus are kept at the Naturalis Biodiversity Center.

Although the sample from Kedung Brubus itself was limited in size, four specimens were added to the dataset that came from other localities in the same region that were also considered part of the Kedung Brubus biostratigraphic unit. This was the case for one specimen from the foot of Butak Hill very close to the Kedung Brubus type site. Butak is stratigraphically composed of alternating tuff- and sandstone layers and bears fossils typical of this fauna (van Heekeren 1957). A second specimen came from Bangle, approximately 12 km north of Kedung Brubus, and is also biostratigraphically placed under the Kedung Brubus unit (Brongersma 1937). This little known site on the Solo River was excavated by Dubois and is part of the Southeast Asian collections of the Naturalis Biodiversity Center. The fossil from Bangle was identified as *Cervus kendengensis*. A third fossil came from Sembungan, found somewhat further to the north of Kedung Brubus, but also within the Solo River Basin. Although the age of the deposit is controversial, the faunal spectrum is suggestive of a similar Middle Pleistocene age as Kedung Brubus (van den Bergh *et al*. 2014). This cervid specimen

was not further taxonomically identified, but probably of the genus *Cervus* (personal observation), and is currently kept at the Geological Museum of Bandung. A final fossil of this kind that was included in the dataset came from Banuraja, a site on the banks of the Citarum River, more to the west of Kedung Brubus (Aziz & de Vos 1999). The site was discovered and first described by Stehn and Umbgrove (1929) and is probably of fluviatile origin (Aziz & de Vos 1999). Based on biostratigraphic arguments, the site is considered similar in age to Kedung Brubus (Aziz & de Vos 1999). The cervid specimen was placed under the nomen *Cervus kendengensis* and is stored at the Naturalis Biodiversity Center.

The second largest fossil sample used in this study (N=16) came from Sangiran. Although von Koenigswald (1940) excavated at Sangiran, the material included here comes from the 1970's Japanese-Indonesian campaign (Watanabe *et al.* 1985) of which the resulting fossils are kept at the Geological Museum of Bandung. This *Homo erectus* site lies north of Soerakarta and is formed by a dome shaped anticline lying between the volcanoes Mount Merapi and Mount Lawu (Indriati & Anton 2008). As opposed to the other sites described here, Sangiran has a long chronological sequence covering multiple biostratigraphic units, ranging from 0.2 to 2.6 Ma (Bouteaux 2005). Of the four formations exposed at Sangiran (see section 3.5.2.3), the Kabuh formation, which is separated from the Pucangan formation by the Grenzbank, is the richest in fossils (Indriati & Anton 2008). Based on biostratigraphic arguments, the cervids included here are all thought to come from the Kabuh formation or the Grenzbank, and are part of the Trinil (H.K.) or Kedung Brubus biostratigraphic unit.

As the exact provenance of the fossils from Sangiran is unknown (Larick *et al.* 2001, Indriati & Anton 2008) it is unclear whether the studied cervids were part of the Upper Kabuh formation (Kedung Brubus unit) or Lower Kabuh formation/Grenzbank (Trinil H.K. unit). Some of the specimens (N=3) were nevertheless catalogued as part of the older Grenzbank

layers and may be correlated with the Trinil H.K. fauna. In terms of species diversity, a substantial number of taxa have been described from Sangiran (see section 4.4.2), such as *Cervus zwaani* (von Koenigswald 1934), *Muntiacus muntjak* (von Koenigswald 1934) and *Axis lydekkeri* (Moigne *et al*. 2004a, 2004b), but the specimens collected during the Japanese-Indonesian campaign were not identified below family level. While it is possible that some of these originally described forms are taxonomically obsolete (Gruwier *et al*. 2015), large sized species (cf. *Cervus* (*Rusa*) sp.) as well as medium sized species (cf. *Axis* sp.) were present in the collection used here (personal observation). It is therefore assumed that at least one form of *Axis* sp. and one form of *Cervus* (*Rusa*) sp. are represented in the Sangiran collection.

6. Results

6.1 Introduction

In section 6.2 the results of the extant cervid ecomorphological analyses were presented for the calcaneus and the intermediate phalanx. After providing the results of error testing for the two models and discussing the results of two preliminary PCA's that deal with the effects of sexual dimorphism and the differences between anterior and posterior specimens (only phalanges), the results of the PCA on all specimens, were discussed. Although the habitat/locomotion groups used in this analysis were already described in chapter 5, a short review of the categories used for the two elements is given in Table 6.1.

Based on a on a broken stick model of eigenvalue distributions and on the accumulative percentage of explained variance a number of relevant components were retained for further analysis (see section 5.5). An NPMANOVA was run on these relevant components to determine statistical significance between predefined groups in the dataset as a whole. Shape changes observed in the thin plate spline deformation grids associated with the axes of the first four principal components were discussed for the two elements. Only those shape differences that were obvious in the deformation grids were further assessed. Visualization of morphological variation along the axes was provided together with the PCA scatterplots and also illustrated in a separate scheme for each principal component.

PCA scatterplots were discussed in terms of specimen patterns and relationships to the observed shape changes. Statistical significance between groups along individual axes was determined using a Kruskal-Wallis test on the PC-scores. The results of a number of ordinary least squares regression analyses, with shape variables regressed against log centroid size, were provided to account for allometric effects. Finally the possible role of a phylogenetic effect was accounted for by visually assessing PCA scatterplots after specimens were

taxonomically labelled and the mean scores for each species calculated for the different axes. A phylogenetic generalized least squares regression was run on the relevant principal components to quantify the overall phylogenetic effect in the dataset.

Type 1	Associated with relatively dry, open environments. Cursorial escape strategy. Limited splaying.
Type 2	Intermediate between type 1- and type 3.
Type 3	Associated with relatively wet, closed environments. Saltatorial escape strategy. More splaying.
Type 4	Associated with mountain environments, saltatorial but with high endurance and speed. More splaying.
Type 5	Associated with open wetland, cursorial but less reliance on speed/endurance than type 1. More splaying.
Type 6*	Associated with tundra habitat, cursorial. More splaying. (*only for the phalanx)

Table 6.1: Short review of habitat/locomotion groups used for the calcaneus and intermediate phalanx

Section 6.3 presented the results of the ecomorphological analyses of the fossil specimens. It was divided in four sub-sections dealing with fossil datasets from different faunal units, sites and extinct species. In section 6.3.1.1, the results of the material from Trinil were discussed, followed in section 6.3.1.2 by the results of an analysis of the species most commonly associated with this site: *Axis lydekkeri*. Section 6.3.1.3 discussed the results of an analysis of *Cervus kendengensis* fossils from several sites associated with the Kedung Brubus faunal unit. In section 6.3.1.4 the results of an analysis of materials from Sangiran was presented. The results for the phalanges (6.3.2) were organized in a similar way, with the exception of section 6.3.2.3. This section also dealt with *Cervus kendengensis* and the Kedung Brubus faunal unit, but was composed of material from other localities (see section 5.8.2). For all combined datasets (extant plus fossil specimens) the appended file was resubmitted to a new GPA and a bg-PCA was conducted on the new procrustes residuals. The same number of principal components were retained as in the extant species analysis, but only those axes that were considered to primarily summarize functionally driven morphological variation, were discussed in detail. PCA scatterplots were visually assessed and statistical significance between pre-assigned groups (along individual axes) was tested using a Kruskal-Wallis test. Differences in multidimensional space were further assessed using a NPMANOVA.

6.2 Results extant specimens

6.2.1 Calcaneus

6.2.1.1 Error testing

Close clustering of replicates in the PCA of the specimens used in the digitization error test (Appendix D) suggested that the protocol used for scanning and creating the surface models for the calcaneus, did not result in large errors. The replicates of the same individuals consistently plotted out closely together and often overlapped in the scatterplot, indicating this error did not have a confounding effect on normal biological variation. Similarly, an intra-observer test revealed that specimen replicates in a second PCA on a group of five individuals formed close clusters in the scatterplot (Appendix D). Following Adriaens' (2007) protocol this indicated that variation in the placement of landmarks over the course of several months of data collection did not obscure normal biological variation.

6.2.1.2 Sexual dimorphism

An exploratory PCA on a dataset of ten *Dama dama* specimens of known sex (Appendix E) revealed no clear visual separation between male and female specimens. Furthermore, an NPMANOVA on the first four components confirmed that male-female separations were non-significant (p=0.734). Based on these results and on analyses in previous studies (Curran 2009, 2012), it could be concluded that shape related sexual dimorphism was minimal in the calcaneus and did not obscure phylogenetic and functional patterns to a large extent.

6.2.1.3 Results PCA

The results of the between groups PCA provided reasonable visual separation along the axes of the first four principal components. Because in the between groups PCA, the eigenanalysis

was run on the five group means, only four principal components were calculated from the original data (as the number of calculated components in this analysis is n-1, where n is the number of datapoints). Because of this reason and since the broken stick distribution of the eigenvalues (see Appendix G) suggested that all four components were relevant, PC1 to PC4 (together summarizing 99.8% of the total variance) were retained for further analysis.

Non parametric MANOVA

The results of the NPMANOVA indicated highly significant differences between the groups (F=4.35, p=0.0001). Pairwise comparisons (Table 6.2) showed that type 1 specimens were significantly different from type 2 (p=0.0018), type 3 (p=0001), type 4 (p=0.0009) and type 5 specimens (p=0.0001). Although type 2 specimens were significantly different from type 1 specimens (p=0.0018), they were not different from type 3 specimens (p=0.2285). These were the only groups that did not give significant separations and indicated that type 2 specimens were more similar in morphology to type 3 specimens as far as the shape differences described by the PCA were concerned. In addition, type 2 specimens were also significantly different from type 4 (p=0.0011) and type 5 specimens (p=0.0017). Besides being significantly different from type 1 specimens, type 3 specimens were also significantly different from type 4 (p=0.0004) and type 5 specimens (p=0.0001). Furthermore, type 5 specimens were found to be significantly different from the type 4 group (p=0.0001).

	Type 1	Type 2	Type 4	Type 3	Type 5
Type 1		**0.0018**	**0.0009**	**0.0001**	**0.0001**
Type 2	**0.0018**		**0.0011**	0.2285	**0.0017**
Type 4	**0.0009**	**0.0011**		**0.0004**	**0.0001**
Type 3	**0.0001**	0.2285	**0.0004**		**0.0001**
Type 5	**0.0001**	**0.0017**	**0.0001**	**0.0001**	

Table 6.2: p-values of pairwise comparisons of an NPMANOVA on the first four principal component scores of a between groups PCA on the calcaneus dataset, with significant values (p<0.05) in bold.

Scatterplots and thin plate spline deformation grids

PC1 summarized 73% of the total variance in the between groups PCA. As expected, a very large part of the shape variance was concentrated in the first component. Visual assessment of the morphological variation summarized by PC1 revealed two main shape changes (Fig. 6.1). A first shape change was a difference in height and angle of the tuber calcanei relative to the articular surfaces of the element. Specimens with a more positive score had tuber calcanei that were positioned more perpendicular relative to the anterior part of the bone with the articular surfaces, as a result of a different orientation of the articular surface supporting the astragalus. Specimens with a negative score had tuber calcanei that were positioned at approximately the same height as the anterior part of the calcaneus. This variation in angle of the tuber calcanei appears to be linked to the hypothesis that in more cursorial forms the calcaneus is expected to be more vertically placed relative to the hindleg in order to achieve a higher pace of contraction during locomotion. A more horizontal tuber calcanei is expected in saltatorial species. Such a shape provides slower contraction but more powerful movement, ideal for leaping. Based on the thin plate spline deformation grids, this observed shape difference could be interpreted as functional.

A second shape change summarized by PC1 was the length of the tuber calcanei itself, relative to the anterior part of the element with the articular surfaces. Specimens with a high score tended to have calcanei that had relatively short tuber calcanei. Specimens with a lower score, on the other hand, had relatively long tuber calcanei. This shape difference was related to the functional hypothesis that the length of this part of the calcaneus is linked to differences in locomotor strategy. As with the angle of the tuber calcanei, the length of the tuber also has an influence on power and speed of contraction in the hock joint. An increased lever arm provides more powerful movement, ideal for saltatorial forms. A shortened lever arm allows

for faster contraction and increased acceleration and is more suitable for cursorial forms. The interpretation of this shape difference would suggest a functional interpretation.

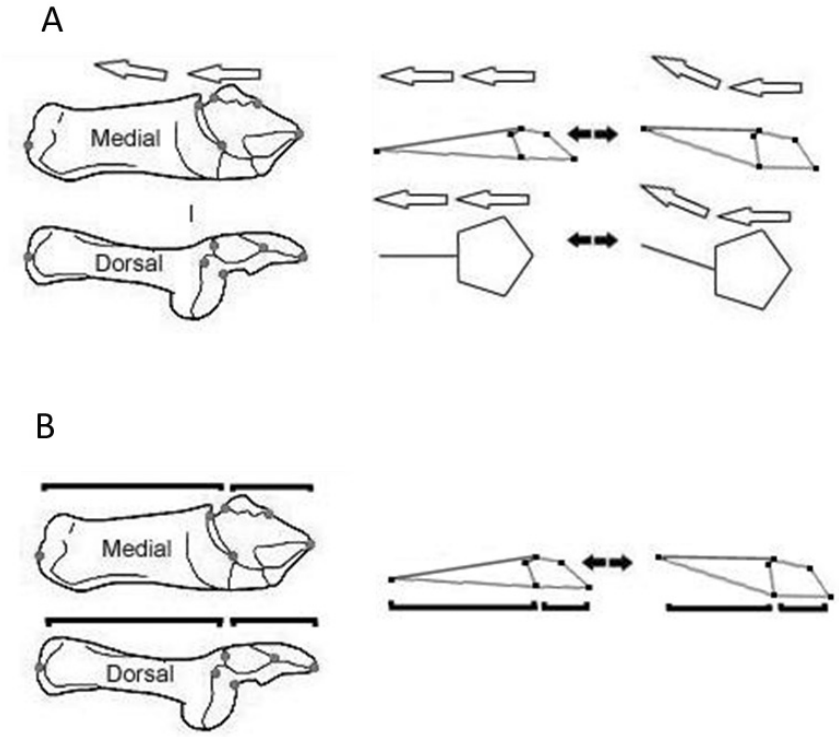


*Figure 6.1: Shape changes observed along PC1 of a bg-PCA on all specimens, with visualizations of the calcaneus all from medial perspective, unless stated otherwise. The illustrations on the right present landmark configurations registered on the calcaneus, the illustrations on the left; their corresponding positions on the bone. In "**A**" a difference in angle of the tuber calcanei, relative to the anterior portion of the calcaneus is presented. Specimens with a high score on PC1 (top, far right) had a tuber positioned at an increased angle relative to the anterior portion of the bone. Specimens with a low score on PC1 (top, second from the right) had a tuber positioned at approximately the same height as the anterior portion of the calcaneus. In "**B**" a difference in length of the tuber calcanei is illustrated. Specimens with a low score on PC1 (bottom, second from the right) had a long tuber relative to the size of the whole bone. Specimens with a high score on PC1 (bottom, first from the right) had a short tuber relative to the size of the whole calcaneus.*

The assessment of the scatterplots associated with PC1 suggested that the trends predicted by the functional hypotheses were partially confirmed by specimen distribution along this axis (Fig. 6.2 and 6.3). Despite substantial overlap, when PC1 was plotted against PC2 (Fig. 6.2), groups showed the highest amount of visual separation. When PC1 was plotted against PC3 (Fig. 6.3), separation was mainly driven by PC1.

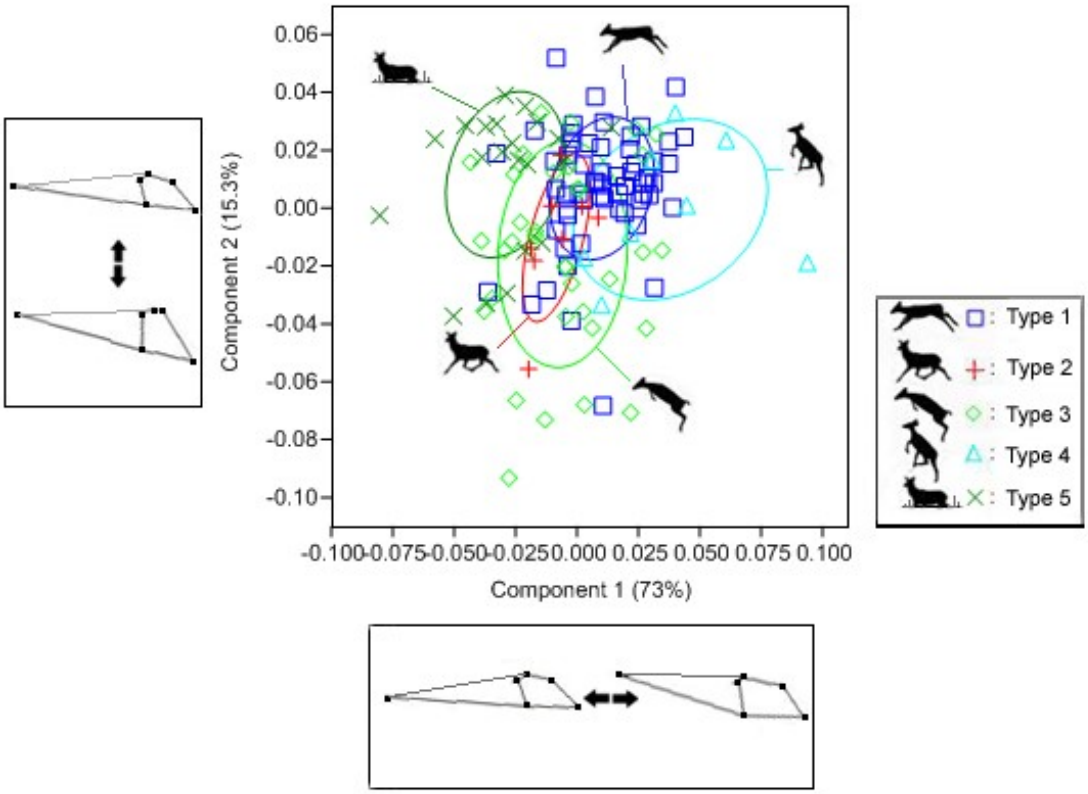


Figure 6.2: PC1 and PC2 scatterplot of a bg- PCA of all specimens ordered by habitat/evasion strategy with 50% confidence intervals.

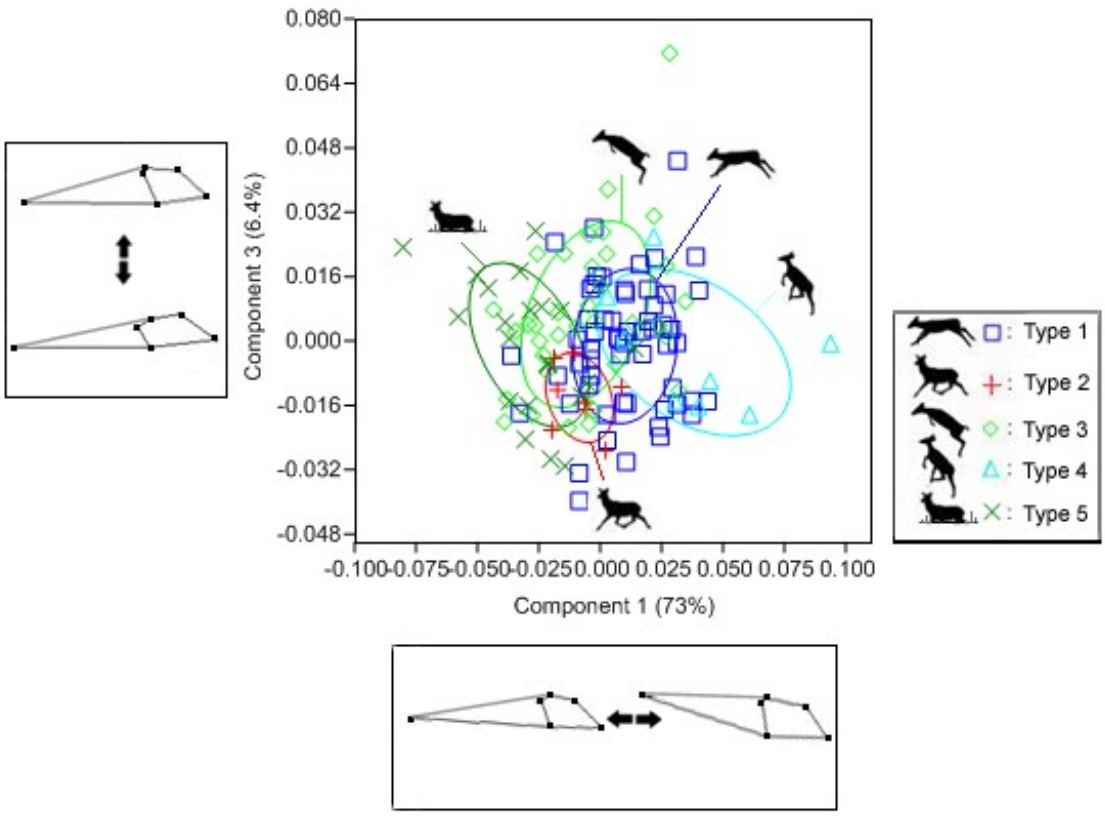


Figure 6.3: PC1 and PC3 scatterplot of a bg- PCA of all specimens ordered by habitat/evasion strategy with 50% confidence intervals.

Type 1 specimens (cursorial/open) tended to have a high score on PC1. Type 3 specimens (saltatorial/closed) also behaved as predicted and tended to give a low score on the first axis. Statistically significant differences between group medians were indicated by the Kruskal-Wallis test (H=53.08, p<0.0001), and pairwise comparisons showed a significant difference between the type 1 and type 3 groups (p=0.0006) (Table 6.3). This implied that the type 1 and type 3 groups had morphological characteristics predicted to be associated with specimens of their habitat and/or locomotor strategy. Type 2 specimens, being intermediate between type 1 and type 3 specimens, visually gave intermediate scores as predicted. This group was found to be significantly different from the type 1 group (p=0.0025), but not from the type 3 group (p=0.7908), indicating its shape was more similar to the saltatorial/closed habitat specimens

(type 3). This pattern generally corroborated the primarily functional interpretation of the thin plate spline deformation grids associated with this shape variable.

Type 4 specimens (saltatorial/high altitude) gave high scores most similar to type 1 specimens, or even higher. The group of type 4 specimens was significantly different from the type 1 (p=0.0061), type 2 (p=0.0013), type 3 (p=0.0004) and type 5 groups (p<0.0001). This, nevertheless, suggested this group was most similar on average to the type 1 specimens. Type 4 specimens were, however, expected to behave more like type 1 specimens (cursorial/open) in the scatterplot due to their tendency to prefer relatively flat terrain over steep, difficult terrain (see further explanation in section 7.2).

PC1	Type 1	Type 2	Type 3	Type 4	Type 5
Type 1	-	**0.0025**	**0.0006**	**0.0061**	**<0.0001**
Type 2	**0.0025**	-	0.7908	**0.0013**	**0.0036**
Type 3	**0.0006**	0.7908	-	**0.0004**	**0.0005**
Type 4	**0.0061**	**0.0013**	**0.0004**	-	**<0.0001**
Type 5	**<0.0001**	**0.0036**	**0.0005**	**<0.0001**	-
PC2	Type 1	Type 2	Type 3	Type 4	Type 5
Type 1	-	**0.0161**	**0.0008**	0.3609	0.1017
Type 2	**0.0161**	-	0.6286	0.5635	**0.0299**
Type 3	**0.0008**	0.6286	-	0.2419	**0.001**
Type 4	0.3609	0.5635	0.2419	-	0.2134
Type 5	0.1017	**0.0299**	**0.001**	0.2134	-
PC3	Type 1	Type 2	Type 3	Type 4	Type 5
Type 1	-	**0.0169**	0.0607	0.6303	0.7687
Type 2	**0.0169**	-	**0.0025**	0.1278	**0.0428**
Type 3	0.0607	**0.0025**	-	0.1746	0.2568
Type 4	0.6303	0.1278	0.1746	-	0.643
Type 5	0.7687	**0.0428**	0.2568	0.643	-
PC4	Type 1	Type 2	Type 3	Type 4	Type 5
Type 1	-	0.2843	0.2205	0.0579	**0.0005**
Type 2	0.2843	-	0.6286	0.5635	0.2134
Type 3	0.2205	0.6286	-	0.2546	**0.044**
Type 4	0.0579	0.5635	0.2546	-	0.8644
Type 5	**0.0005**	0.2134	**0.044**	0.8644	-

Table 6.3: p-values of Mann-Whitney pairwise comparisons of a Kruskal-Wallis test for PC1 to PC4 of the bg-PCA on all extant calcanei with significant values (p<0.05) in bold.

Type 5 specimens (cursorial/open wetland) were visually well separated from the main luster of datapoints. This group was found to be significantly different from the type 1 (p<0.0001), type 2 (p=0.0036), type 3 (p=0.0005) and type 4 specimens (p<0.0001). In the PCA, this group produced prominently negative scores, most similar to the type 2 and type 3 groups. This indicated that their morphology, as summarized by PC1, was more similar to that of intermediate- and saltatorial (closed habitat) species. Although in the functional hypotheses (see chapter 5) it was predicted that type 5 specimens would be morphologically similar to the more cursorial type 1 specimens, this pattern could perhaps be explained by the fact that sufficient cover is still present in the open wetlands that type 5 species inhabit (see further explanation in section 7.2).

Overall, specimen between-group relationships along the first component implied that shape variation along this axis was to a substantial extent functionally driven. This is mainly suggested by a gradient in shape from type 1, over type 2, to type 3 species. In addition, the placement of type 4 and type 5 specimens could also potentially be explained as a result of functional differences.

PC2 was responsible for 15.3% of the total variance. The primary shape difference that was observed along the second axis was a difference in length of the articular surface that supports the malleolus (Fig. 6.4). In specimens with a high score, the articular surface tends to be longer and in specimens with a low score it tends to be shorter in the anterio-posterior direction. This could be related to the functional hypothesis that cursorial species are predicted to have a longer articular surface for the malleolus, as this provides more stability when running at high speed. A functional interpretation for this shape difference is therefore not unlikely.

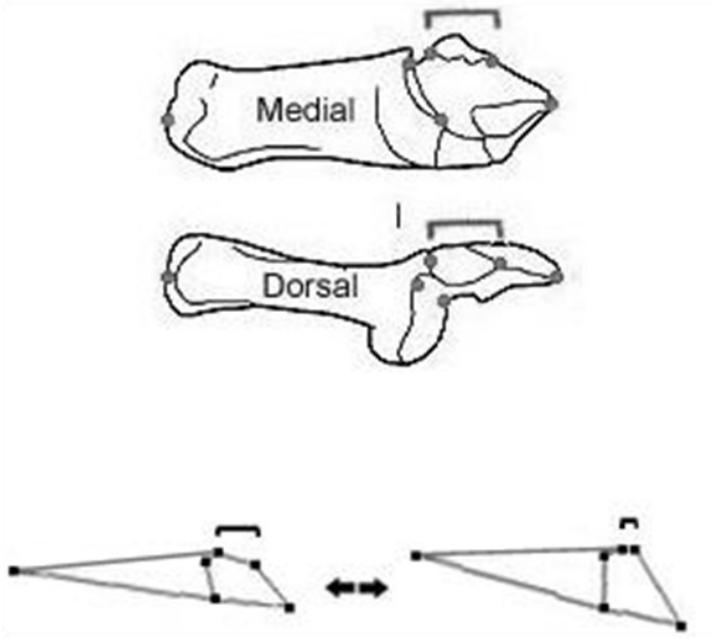


Figure 6.4: Shape changes observed along PC2 of a bg-PCA on all specimens, with visualizations of the calcaneus all from medial perspective, unless stated otherwise. The illustrations at the bottom present landmark configurations registered on the calcaneus, the illustrations on the top; their corresponding positions on the bone. In the schematic a difference in the size of the articular surface with the malleolus is illustrated. Specimens with a high score on PC2 (bottom right) had a relatively short articular surface supporting the malleolus. Specimens with a low score on PC2 (bottom left) had a relatively long articular surface supporting the malleolus.

Even though on the second axis visual separation in the scatterplot was not as good as on the first axis, the predefined groups were still clearly distinct (Fig. 6.2 and 6.5). Separations appeared to be best when the second component was plotted against the first component, but were mainly driven by the first axis (Fig. 6.2). When PC2 was plotted against PC3, separations on the second axis were less obscured than in the first scatterplot (Fig. 6.5).

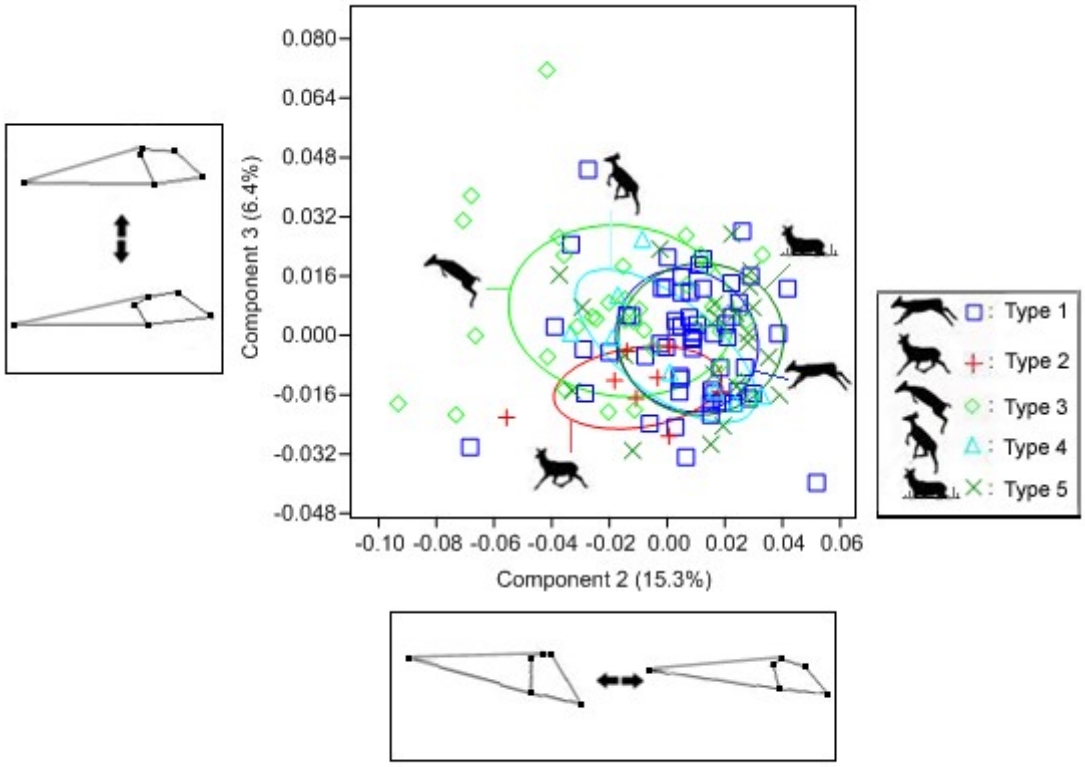


Figure 6.5: PC2 and PC3 scatterplot of a bg- PCA of all specimens ordered by habitat/evasion strategy with 50% confidence intervals.

Type 1 specimens (open/cursorial) tended to give a high score on PC2, while type 3 specimens (closed/saltatorial) gave a lower score. The Kruskal-Wallis test indicated that overall differences between group medians were highly significant (H=19.36, p=0.0006) and pairwise comparisons showed significant differences between the type 1 and type 3 specimens (p=0.0008) (Table 6.3). Type 2 specimens appeared intermediate between type 1- and type 3, but were only significantly different from the former (p=0.0161) and not the latter group (p=0.6286). This means that type 1 specimens had a relatively long articular surface supporting the malleolus, as was expected for this group. In type 3 specimens this articular surface was shorter, while in type 2 specimens, it was intermediate between type 1 and type 3, but probably more similar to the type 3 group.

Type 5 specimens (cursorial/open wetland) were not well separated on the second axis and gave results similar to type 1 specimens in the PCA. According to the pairwise comparisons of the Kruskal-Wallis test (Table 6.3) this group was significantly different from type 2 (p=0.0299) and type 3 specimens (p=0.001), but not from type 1 (p=0.1017) and type 4 specimens (p=0.2134).The location of this group in the scatterplot as far as the articular surface of the malleolus is concerned, is not necessarily surprising. This is a morphological aspect predicted to be found in animals with a more cursorial locomotor strategy, also found in type 1 specimens. It is nevertheless somewhat contradictory to the pattern described by this group along the first axis. In PC1, type 5 specimens gave scores more similar to the type 2 and type 3 specimens, although differences from these groups were still significant.

Type 4 specimens (saltatorial/high altitude) also gave a similar score to type 1 specimens as in most other scatterplots of the PCA. The length of the articular surface for the malleolus was therefore probably more similar in shape to cursorial species and not, to the more saltatorial type 3 species. No significant differences between the type 4 group and the other groups were found though (Table 8). Overall the scatterplots associated with PC2 suggested that the shape differences summarized by this axis may be at least partially functional, although other confounding factors such as allometry or phylogeny could play a role, too (see below).

PC3 explained 6.4% of the total variance. Two main shape differences were observed during visual assessment of the thin plate spline deformation grids associated with the third axis (Fig. 6.6). A first shape change (Fig. 6.6) summarized by PC3 was the size of the posterior talar articular surface. Specimens with a more positive score had larger posterior talar articular surfaces, while in specimens with a negative score this articular surface was smaller. No clear link can be made with any of the proposed functional hypotheses, but the size of this articular surface could perhaps also be associated with joint stabilization, as is probably the case for the

articular surface supporting the malleolus, a shape change described along the second axis. A second shape change (Fig. 6.6) summarized by PC3 was a variation in the distance between the articular surface of the malleolus and the posterior talar articular surface. In specimens with a low score the distance between these two articular surfaces was high. In specimens with a high score, the distance between the articular surfaces was limited. Based on the thin plate spline deformation grids it could not be concluded that there was a clear link between this morphological difference and any of the proposed functional explanations.

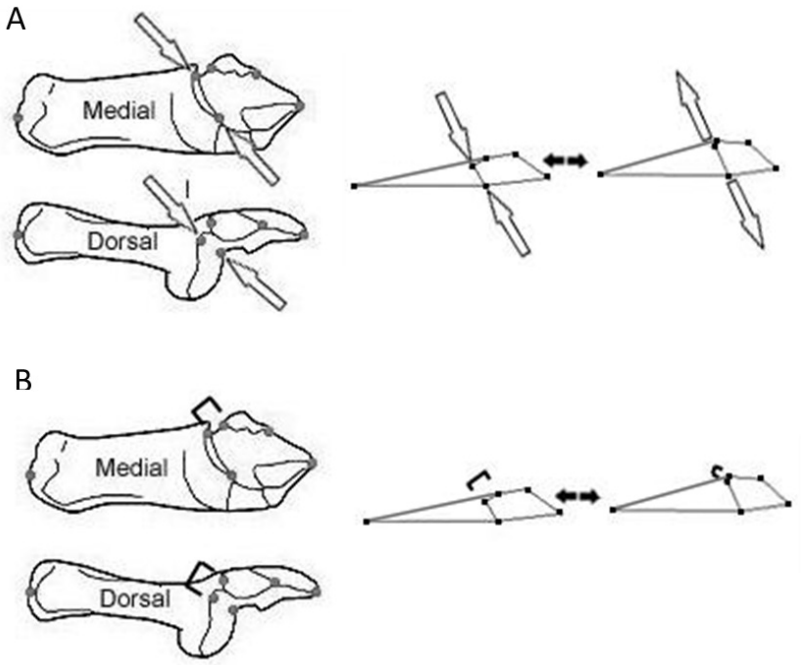


*Figure 6.6: Shape changes observed along PC3 of a bg-PCA on all specimens, with visualizations of the calcaneus from medial perspective, unless stated otherwise. The illustrations on the right present landmark configurations registered on the calcaneus, the illustrations on the left; their corresponding positions on the bone. In "**A**" a difference in size of the posterior talar articular surface is presented. Specimens with a high score on PC3 (top, far right) had a posterior talar articular surface that was relatively long in the proximo-distal direction. Specimens with a low score on PC3 (top, second from the right) had a posterior talar articular surface that was shorter in the proximo-distal direction. In "**B**" a difference in the distance between the posterior talar articular surface and the articular surface supporting the malleolus is shown. In specimens with a high score on PC3 (bottom, far right), the distance between the two articular surfaces was small. In specimens with a low score on PC3 (bottom, second from the right), the distance between the two articular surfaces was large.*

Unsurprisingly, the third component did not show as good visual separation in the scatterplot as the first two components. When plotted against PC1 (Fig. 6.3) and PC2 (Fig. 6.5) it was mostly the other components that drove the separations. In the scatterplot with PC4 no clear pattern was observed and all specimens clustered together in the center (Fig. 6.7). Nevertheless, statistically significant differences were found in the Kruskal-Wallis test of the scores of PC3 (H=11.24, p=0.024). Furthermore, pairwise comparisons indicated significant differences between the type 2 group and the type 1 (p=0.0169), type 3 (p=0.0025) and type 5 groups (p=0.0428). As the scatterplot generally did not result in clear separations and the deformation grids did not suggest a clear link with any of the functional hypotheses, there does not appear to be a clear functional signal summarized by this component.

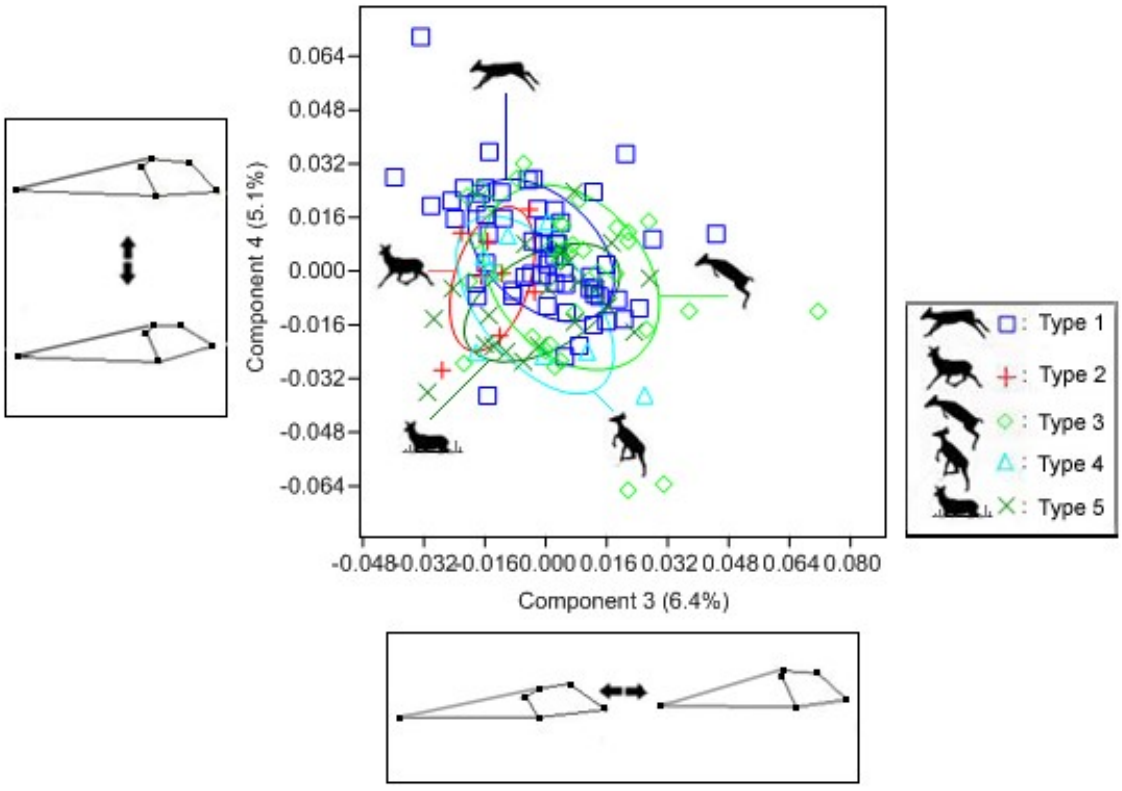


Figure 6.7: PC3 and PC4 scatterplot of a bg- PCA of all specimens ordered by habitat/evasion strategy with 50% confidence intervals.

PC4 was responsible for 5.1% of the variance. The main shape difference that was observed along the axis of PC4 was a difference in height of the anterior end of the articular surface with the cubonavicular (Fig. 6.8). In specimens with a low score it was positioned comparatively high relative to the rest of the calcaneus. In specimens with a high score it was positioned lower relative to the rest of the calcaneus. Possibly this had an effect on the placement of the calcaneus on the cubonavicular and on the positioning of the calcaneus as a whole in the hockjoint. A lower anterior end of this articular surface may place the calcaneus on the cubonavicular in a more vertical position relative to the rest of the hindleg. This more vertical position would be expected in more cursorial forms as it is optimized for quicker but less powerful movements in the joint during contraction. A more horizontal postion of the calcaneus would be expected in saltatorial forms, as this morphotype is associated with slower, but more powerful movement in the joint. This shape difference is nevertheless not as clearly linked with any of the previously formulated functional hypotheses.

In the scatterplot associated with PC4, all specimens clustered together in the center of the graph (Fig. 6.7). Although not clearly visible in the scatterplot, the Kruskal-Wallis test indicated overall significant differences between groups (H=13.43, p=0.0093). Moreover, pairwise comparisons showed significant differences between the group of type 5 specimens and type 1 (p=0.0005) and type 3 specimens (p=0.044) (Table 6.3). Although the deformation grids may indicate a potential connection with the previously formulated functional hypotheses, the weak separations associated with this shape variable are not in support of a strong functional signal.

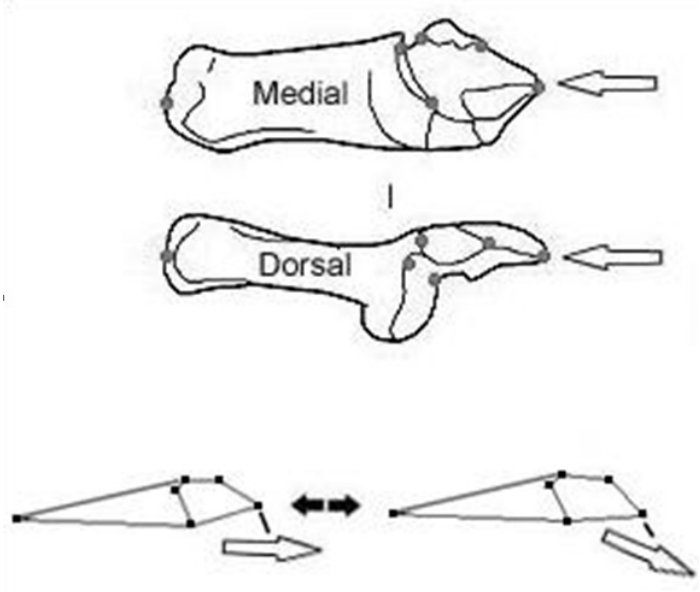


Figure 6.8: *Shape changes observed along the axis of PC4 of a bg-PCA on all specimens, with visualizations of the calcaneus all from medial perspective, unless stated otherwise. The illustrations at the bottom present landmark configurations registered on the calcaneus, the illustrations on the top; their corresponding positions on the bone. In the schematic a difference in the height of the anterior end of the articular surface with the cubonavicular is shown. In specimens with a high score on PC4 (bottom right), the anterior end of the articular surface with the cubonavicular was placed lower, relative to the rest of the bone. In specimens with a low score on PC4 (bottom left), the anterior end of the articular surface with the cubonavicular was placed higher, relative to the rest of the calcaneus.*

Allometry

The results of the ordinary least squares regressions against log centroid size suggested that some of the principal components may be partially driven by allometric size effects. Fitted line plots can be found in Appendix H. When PC1 was regressed against log centroid size a significant, but very weak, correlation was found between shape and centroid size (R^2=0.0414, p=0.0202). This implied that only a small amount of the shape variance explained by PC1 could be attributed to an allometric effect. A similar result was found for PC2. A regression of the second component against centroid size gave a significant, but weak

correlation between the shape- and size variables (R^2=0.0306, p=0.0462). As in the first component, only a small amount of the variance in shape summarized by PC2 could be attributed to allometric differences. The regression on the third component did not reveal a significant correlation with size (R^2=0.005, p=0.4199), implying that the allometric effects of size difference had little to no effect on this component. In PC4 on the other hand, the allometric effect was potentially the strongest. The regressions resulted in a highly significant, although relatively weak, correlation with log centroid size (R^2=0.0975, p<0.001). This implied that, in comparison with the other components, PC4 was subject to a more substantial, although still fairly small, allometric effect.

Phylogeny

A phylogenetic generalized least squares regression on the relevant principal components (PC1 to PC4) indicated that phylogeny may have also contributed to the shape differences summarized by the PCA. The PGLS regression resulted in a high pagel's λ (0.906), but one that was not significantly different from 1 ($p(H_0:\lambda=1)$=0.2902) or from 0 ($p(H_0:\lambda=1)$=0.3227). These results indicated that there was a phylogenetic signal in the dataset. However, as p-values were not significantly different from the upper (1) and lower bound (0), it was likely that phylogenetic relatedness was only partially responsible for the morphological differences summarized by the between groups PCA. It was reasonable to assume that functional differences played a role, as well. Full output data and R-scripts were provided in Appendix I.

When re-assessing PCA scatterplots after calculating mean shapes per species, no clear patterns were revealed that would suggest that the morphological differences summarized by the between groups PCA were primarily driven by phylogenetic relatedness (Fig. 6.9, 6.10, 6.11 and 6.12). On the other hand, some closely related taxa clustered together, indicating that phylogeny did play a role.

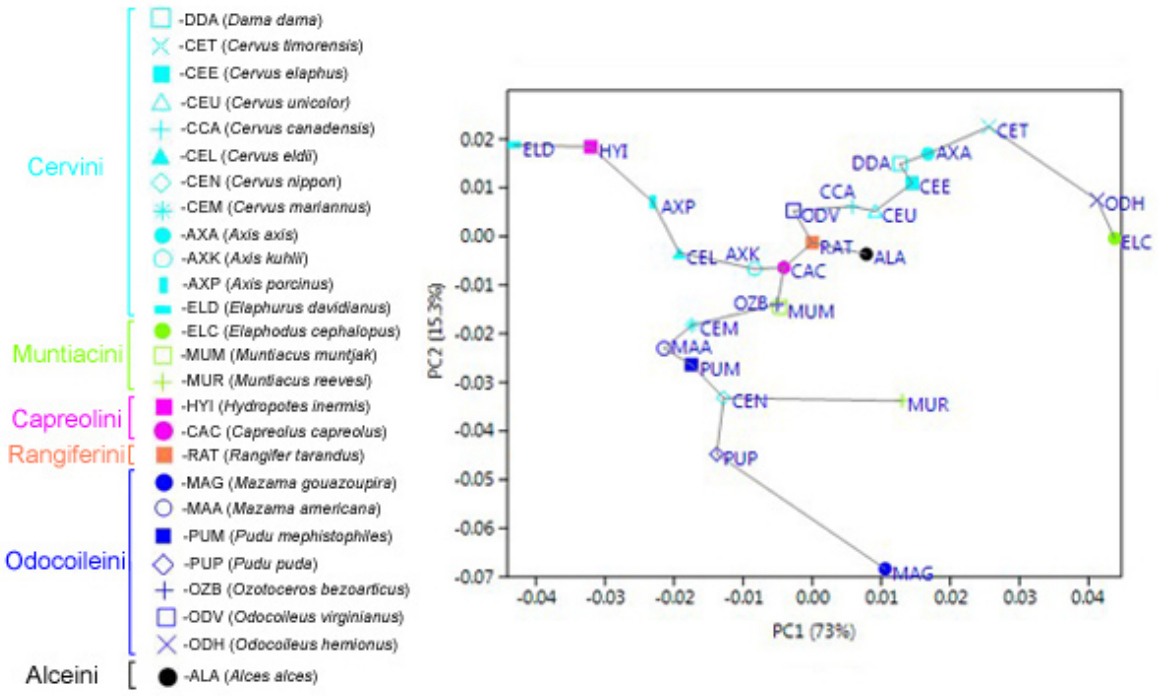


Figure 6.9: Scatterplot of mean shapes per species as described by PC1 and PC2 of a bg-PCA on all calcaneus specimens with minimal spanning tree representing shortest possible distance between data points.

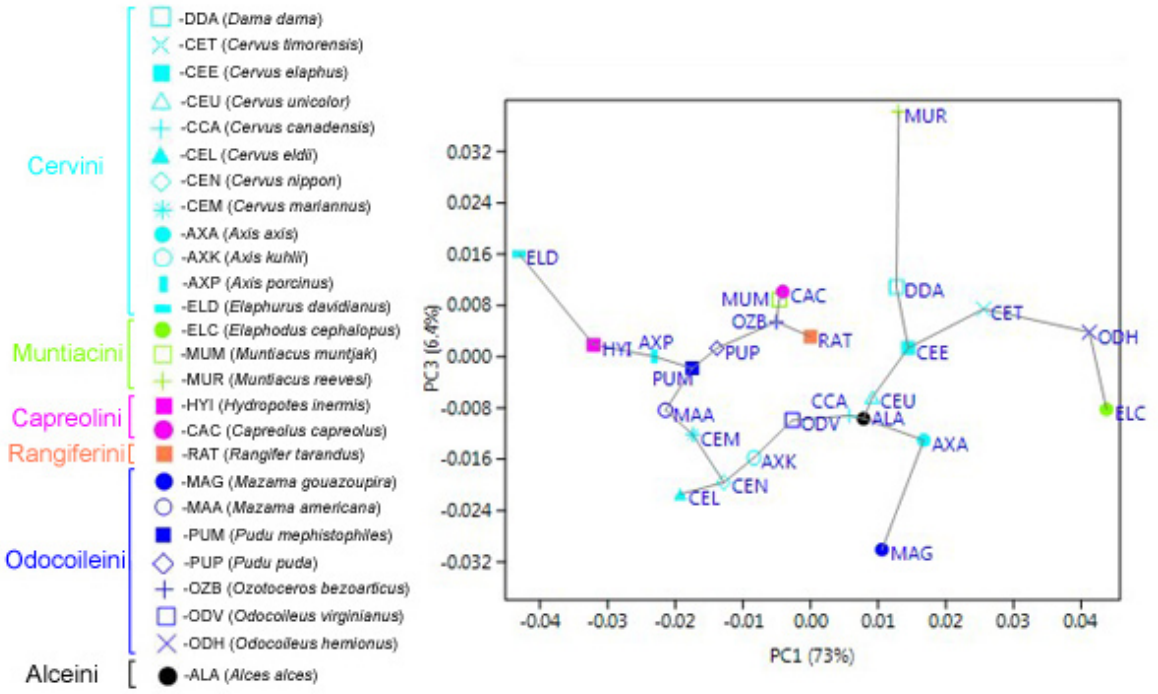


Figure 6.10: Scatterplot of mean shapes per species as described by PC1 and PC3 of a bg-PCA on all calcaneus specimens with minimal spanning tree representing shortest possible distance between data points.

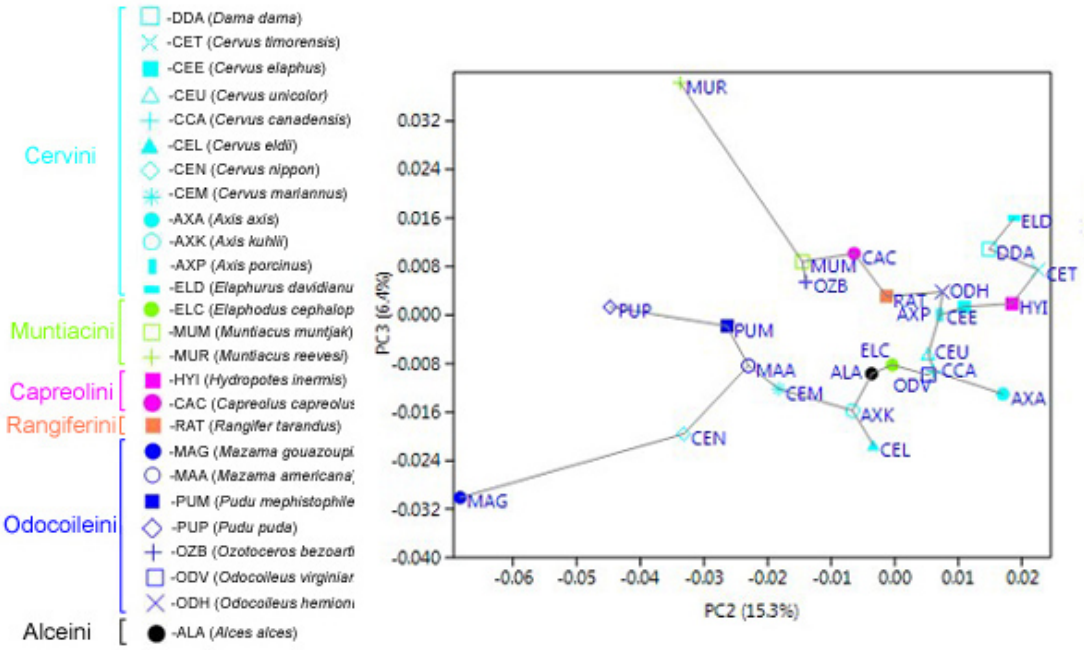


Figure 6.11: Scatterplot of mean shapes per species as described by PC2 and PC3 of bg-PCA on all calcaneus specimens with minimal spanning tree representing shortest possible distance between data points.

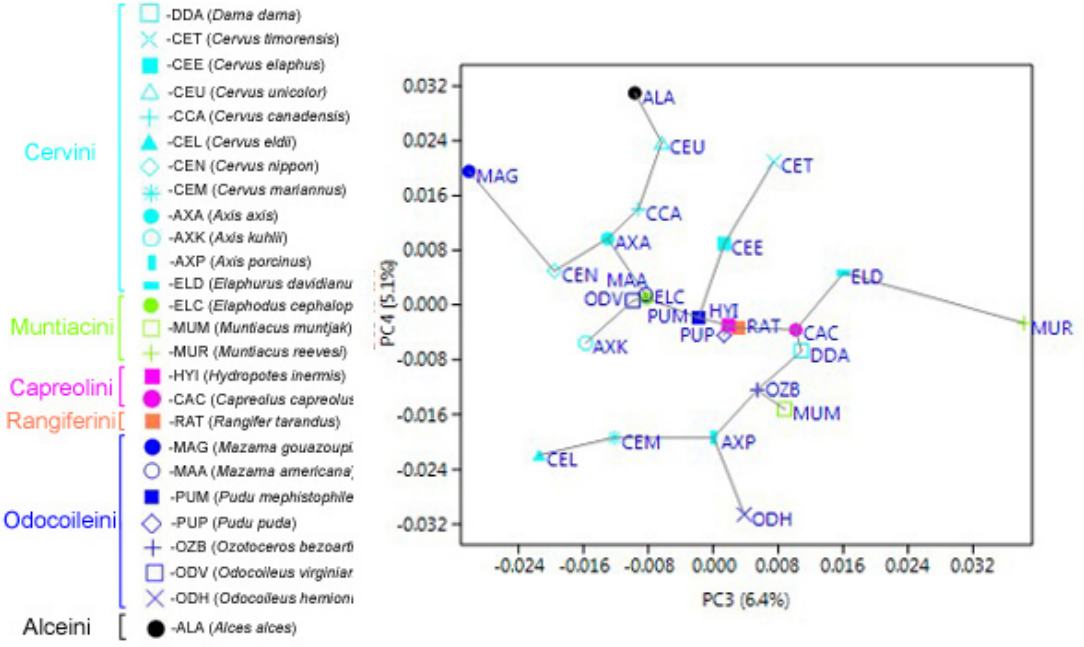


Figure 6.12: Scatterplot of mean shapes per species as described by PC3 and PC4 of a bg-PCA on all calcaneus specimens with minimal spanning tree representing shortest possible distance between data points.

On the first axis, several members of the Cervini tribe gave high scores (Fig. 6.9 and 6.10). Species such as *Cervus elaphus*, *Cervus canadensis*, *Cervus unicolor*, *Cervus timorensis* and *Axis axis* were all found in the upper right corner of the graph when PC1 was plotted against PC2 (Fig. 6.9). Although most of these species can be associated with broadly similar habitats and their corresponding locomotor adaptations, forms such as *C. unicolor* and *C. timorensis* have somewhat different ecological preferences and may be close together due to their phylogenetic relatedness. The members of the Cervini tribe that were associated with a type 5 strategy (cursorial/open wetland), on the other hand, were found in the upper left corner of the graph and clustered well together with type 5 species of other tribes, such as *Hydropotes inermis*. The separation should probably be interpreted as a functional difference. This pattern was less clearly observed on the second and third axes. Although the Cervini still clustered relatively well together there, the distinction between type 1 and type 5 members was not so clear anymore (Fig. 6.9, 6.11 and 36). PC4 did not reveal any clear phylogenetic patterns for this tribe (Fig. 6.12).

The members of the Odocoileini tribe were relatively well separated from the Cervini tribe, with the exception of the genus *Odocoileus*. The main group of smaller (mainly saltatorial) Odocoileini was found in the lower center and lower left corner when PC1 was plotted against PC2 (Fig. 6.9). Despite its atypical habitat- and locomotor adaptations, *Ozotoceros* also clustered with this group. This association might have been driven by phylogeny. The fact that the genus *Odocoileus* clustered more closely with the Cervini might have been functionally driven, though. This pattern was observed along the first two axes (Fig. 6.9, 6.10 and 6.11), but not along PC3 and PC4 (Fig. 6.10, 6.11 and 6.12).

Possibly some members of the Muntiacini tribe clustered together due to phylogenetic relatedness, although it should be mentioned that the members of the genus *Muntiacus* have

fairly similar habitat preferences. When PC1 was plotted against PC2, *Muntiacus muntjak* was still reasonably close to *M. reevesi*, but nevertheless much closer to some other species such as *Capreolus capreolus* and *Cervus mariannus* (Fig. 6.9). On the second axis *Muntiacus muntjak* was at least the closest species to *M. reevesi*, but other, unrelated species (e.g. *C. capreolus*), were again closer to the *M. muntiacus* (Fig. 6.11). On PC3 and PC4 the muntjacs did not cluster together at all (Fig. 6.12). The genus *Elaphodus* gave different scores on all axes and despite its relatedness to *Muntiacus,* never gave similar results (Fig. 6.9, 6.10, 6.11 and 6.12). Probably this pattern was driven by functional differences.

The Rangiferini gave a relatively positive score on PC1 and PC2, similar to the type 1 Cervini (Fig. 6.9, 6.10 and 6.11). The Rangiferini are, however, most closely related to the Odocoileini. The fact that they were more closely positioned to the main group of type 1 specimens would indicate that this group's place on the scatterplot was driven more by functional differences in this case. On PC3 and PC4, on the other hand, it was close to the genera *Pudu* and and *Ozotoceros* too (Fig. 6.10, 6.11 and 6.12). This could be a pattern driven by phylogenetic relatedness.

The Alceini tribe, consisting of *Alces alces* only, was on the first two axes closest to the Rangiferini, the tribe to which it is most closely related. On the first two axes, but not the third, it was also relatively close in shape to the cursorial type1 Cervini (Fig. 6.9, 6.10 and 6.11). Its closeness to the Rangiferini in the first two components could reflect a phylogenetic signal, but the proximity to the cervini on most axes would also indicate that functional similarities played a role in driving this group in the PCA.

The Capreolini, with the genera *Capreolus* and *Hydropotes*, gave very different results on the first two axes of the PCA (Fig. 6.9, 6.10, and 6.11). *Capreolus* gave slightly negative scores on PC1, closest to *Axis kuhlii* and *Muntiacus muntjak*. *Hydropotes* gave scores similar to the

type 5 Cervini. The divide between the two genera was probably mainly functional. On the third and fourth axis the two genera were relatively close together, though (Fig. 6.12).

Overall, it appeared that morphological variation in the first four principal components of the between groups PCA was driven by a combination of function and phylogeny. Some of the closely related taxa had the tendency to cluster together, probably due to phylogenetic relatedness and the PGLS regression indicated that there was certainly a phylogenetic signal present in the dataset. Nevertheless, is seemed clear that many of the larger patterns observed in the PCA were driven by functional differences. Many taxa of the same functional and ecological affinity appeared to cluster together, despite being only distantly related. Although a scenario where each component was driven by a closely intertwined combination of functional and phylogenetic factors was most realistic, it appeared that on the first two axes, and especially in the first component, the functional signal was particularly strong. Such an interpretation was also corroborated by the links that were found between some of the morphological changes observed along the first (and possibly the second) axis and some of the earlier described functional hypotheses about the calcaneus (see further discussion in section 7.2).

6.2.2 Intermediate phalanx

6.2.2.1 Error testing

Replicates in the PCA of the phalanges used in a digitization error test (Appendix D) clustered closely together, suggesting that imprecision in the scanning process, did not result in substantial errors. The replicates of the same individuals consistently plotted out closely together. This indicated that errors resulting from differences between scans did not confound normal biological variation to a large extent. In addition, an intra-observer test revealed that landmarking replicates in a PCA on a group of five individuals also clustered close together in

a scatterplot of the first two components (Appendix D). This implied that variation in landmark-placement over multiple months of data collection did not have a confounding effect on normal biological variation (Adriaens 2007).

6.2.2.2 Sexual dimorphism

An exploratory PCA on a set of ten *Dama dama* specimens of known sex (Appendix E) revealed no clear male-female visual separation on a scatterplot of the first two components. In addition, an NPMANOVA on PC1 to PC4 confirmed that separations between sexes were non-significant (p=0.6677). It could be concluded from these results and from earlier studies on sexual dimorphism in cervid phalanges (Curran 2009, 2012), that shape related sexual dimorphism was limited in the intermediate phalanx and did not obscure phylogenetic and functional patterns.

6.2.2.3 Anterior or posterior position

An exploratory PCA on intermediate phalanges of known anatomical position (anterior/posterior) resulted in limited visual separation between the anterior and posterior elements (Appendix F). Posterior phalanges appeared to give a somewhat higher score on PC2, but the pairwise comparisons of an NPMANOVA on the first four PC-scores (F=15.74, p=0.0001) indicated that differences between phalanges of different anatomical position were non-significant *within* species for *Dama dama* (p=0.1755) and *Capreolus capreolus* (p=0.0658). Visual separation *between* species was on the other hand clear in the scatterplot of PC1 and PC2. This was confirmed by the pairwise comparisons, resulting in significant differences between all species groups: between *C. capreolus* anterior phalanges and *D. dama* anterior phalanges (p=0.0008), between *C. capreolus* anterior phalanges and *D. dama* posterior phalanges (p=0.001), between *D. dama* anterior phalanges and *C. capreolus* posterior phalanges (p=0.0007) and between *D. dama* posterior phalanges and *C. capreolus*

posterior phalanges (p=0.001). Although it should not necessarily be taken from these results that no morphological differences between anterior and posterior phalanges exist, it is indicated by the PCA that the landmarking protocol mainly registered shape variation driven by other factors. As will be further explored in section 6.2.2.4, these are mainly phylogeny and differences in locomotor strategy pertaining to substrate and vegetation type. From the above analysis, it appeared that differences resulting from the anatomical position of the phalanx did not obscure these phylogenetic or ecological signals.

6.2.2.4 Results PCA

The results of a bg-PCA on the procrustes residuals of the intermediate phalanx provided moderate visual separation along the axes of the first four components. As in the calcanei, the eigenanalysis was run on six group means. Only five PC's were calculated from the dataset. Because visual separation was best for the first four axes and because the broken stick distribution of eigenvalues (Appendix G) indicated only the first two PC's were relevant, PC1 to PC4 (together sumerizing 97.2 % of the total variance) were retained for further analysis.

Non parametric MANOVA

The results of an NPMANOVA on the first four components indicated significant between-group differences (F=15.38, p=0.0001). Moreover, pairwise comparisons showed significant differences between type 1 specimens and type 2 (p=0.0052), type 3 (p=0.0001), type 4 (p=0.0259), type 5 (p=0.0001) and type 6 specimens (p=0.0001) (Table 6.4). While type 2 specimens were significantly different from type 1 (p=0.0052), type 3 (p=0.0011) and type 6 specimens (p=0.0001), differences from the type 4 (p=0.2415) and type 5 groups (p=0.0677) were not. Moreover, separations were significant between the type 3 group and the type 4 (p=0.0021), type 5 (p=0.0089) and type 6 groups (p=0.0001), as well as between the type 4 group and the type 5 (p=0.0348) and type 6 groups (p=0.0019). Differences between the type

5 and type 6 groups were highly significant (p=0.0006), as were differences between type 6 and all other groups.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Type 1		**0.0052**	**0.0001**	**0.0259**	**0.0001**	**0.0001**
Type 2	**0.0052**		**0.0011**	0.2415	0.0677	**0.0001**
Type 3	**0.0001**	**0.0011**		**0.0021**	**0.0089**	**0.0001**
Type 4	**0.0259**	0.2415	**0.0021**		**0.0348**	**0.0019**
Type 5	**0.0001**	0.0677	**0.0089**	**0.0348**		**0.0006**
Type 6	**0.0001**	**0.0001**	**0.0001**	**0.0019**	**0.0006**	

Table 6.4: p-values of pairwise comparisons of an NPMANOVA on the first four principal component scores of a between groups PCA on the intermediate phalanx dataset, with significant values (p<0.05) in bold.

Scatterplots and thin plate spline deformation grids

PC1 summarized 47.1% of the total variance in the between groups PCA. A visual assessment of the morphological differences described by this component revealed one clear primary shape difference summarized by this axis (Fig. 6.13). Specimens with a lower score on PC1 generally had a more slender, elongated shape. Specimens with a high score on this axis had a shorter, more robust morphology. A correlation between the gracility of the intermediate phalanx and function and environment was expected in the proposed functional hypotheses. How these factors are connected was nevertheless unclear. According to Köhler (1993) gracile intermediate phalanges are to be expected in cursorial, open environment species.

Degusta and Vrba (2005a, 2005b) on the other hand suggested that gracile phalanges are more typical for species adapted to wet substrate. As Degusta and Vrba (2005a, 2005b) did not give a functional explanation to their prediction, the potential biomechanical reasons behind these morphological differences remain somewhat obscure, but it is likely that this shape difference can at least be partially explained in terms of function. Possibly there is a

link with an increased capacity for splaying the phalanges in species adapted to more yielding substrates.

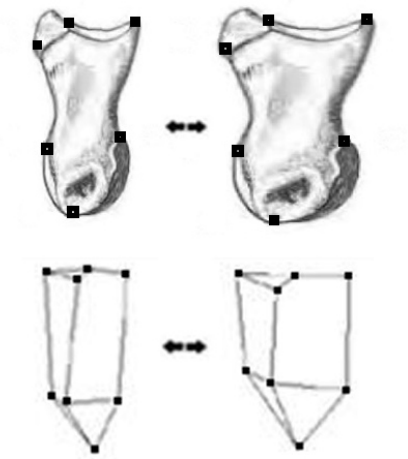


Fig. 6.13: Difference in gracility between phalanges observed along the axis of PC1 of a between groups PCA on all intermediate phalanges, with visualizations of the phalanx all from medial perspective. The illustrations at the bottom present landmark configurations registered on the intermediate phalanx, the illustrations on the top; their corresponding positions on the bone. In the schematic a difference in gracility along the first axis is presented. Specimens with a high score on PC1 (bottom right) were relatively robust, while specimens with a low score on PC1 (bottom left) had a more gracile shape.

An assessment of the scatterplots associated with PC1 suggested that the patterns observed in the thin plate spline deformation grids and the proposed functional hypotheses were at least partially confirmed by specimen and group separations along the axis (Fig. 6.14 and 6.15). Visual overlap between the groups was substantial, but individual clusters could still be clearly discerned in the graph, especially when PC1 was plotted against the second component (Fig. 6.14). When PC1 was plotted against PC3 (Fig. 6.15) visual separation was good, but less clear than in the first scatterplot (Fig. 6.14). Separations were in this case mainly driven by the first axis.

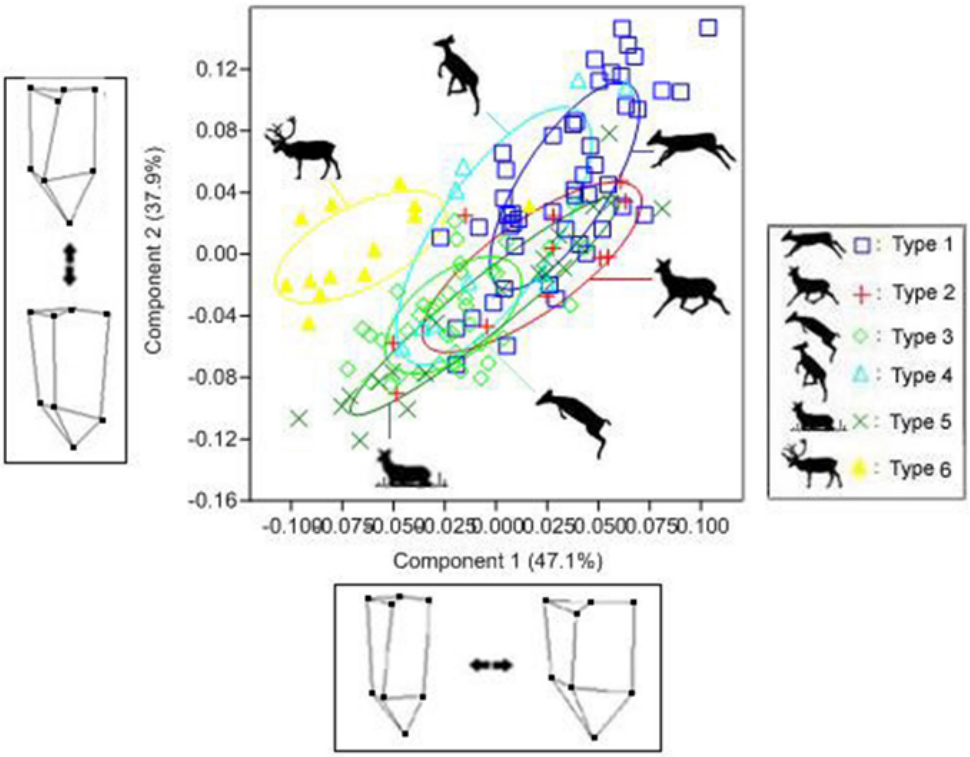


Figure 6.14: PC1 and PC2 scatterplot of a between groups PCA of all extant phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.

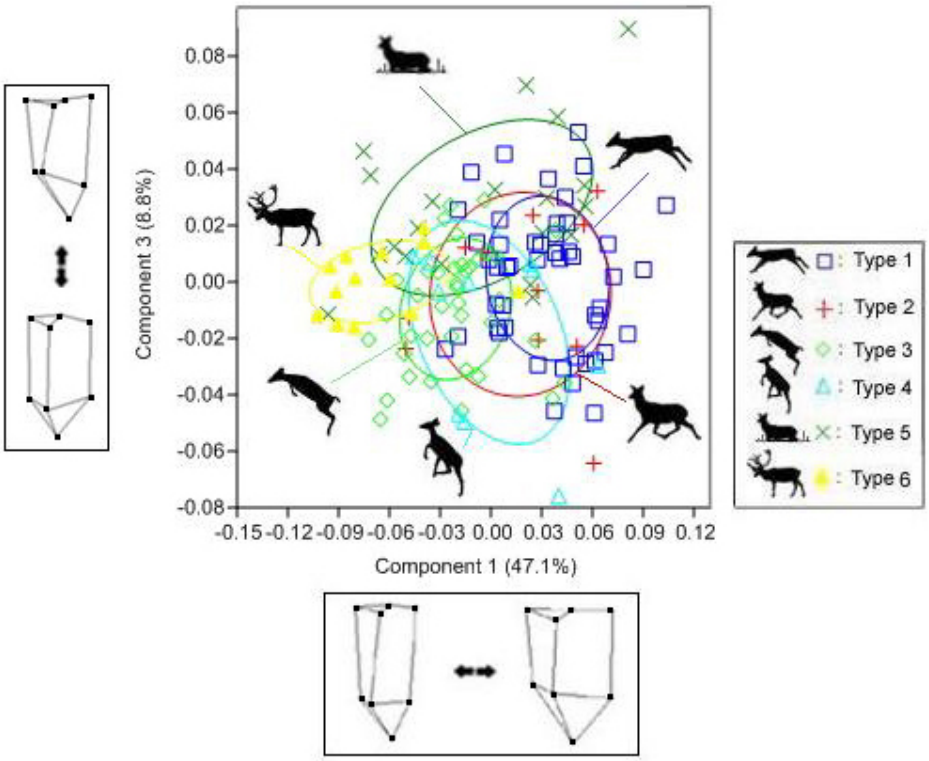


Figure 6.15: PC1 and PC3 scatterplot of a between groups PCA of all extant phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.

As predicted, type 1 specimens (cursorial/open/dry substrate) generally gave a relatively high score on PC1. Type 3 species (saltatorial/closed/wet substrate) on the other hand gave a more negative score on this axis, while the intermediate type 2 species overlapped with the type 1 and type 3 groups. This separation suggested a gradient between type 1, type 2 and type 3 species, as was proposed in the functional hypotheses. The Kruskal-Wallis test indicated statistically significant differences between group medians (H=60.57, p<0.0001). Pairwise comparisons confirmed that the separation between type 1 and type 3 specimens was statistically highly significant (p<0.0001) on the first axis (Table 6.5). The difference between type 2 and type 3 specimens was also significant (p=0.007), but type 2 specimens were not statistically significant from type 1 specimens (p=0.3069). This implied that intermediate type 2 specimens were generally more similar to type 1 species, characterized by cursoriality and by drier, open environments.

Type 4 specimens (saltatorial/mountain) tended to be dispersed across the scatterplot (Fig. 6.14 and 6.15). This was reflected in the pairwise comparisons of the Kruskal-Wallis test (Table 6.5). Type 4 specimens were not significantly different from most other groups (type 2, type 3 and type 5) on the first axis. They were, however, significantly different from the type 1 (p=0.006382) (open/cursorial) and type 6 (tundra/cursorial) (p=0.0004584) groups. This would imply that the shape of the phalanx in mountain adapted type 4 specimens was more similar to that of the type 2, type 3 and type 5 species, groups that were expected to have an increased capacity for splaying the phalanges.

PC1	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Type 1		0.3069	**<0.0001**	**0.0063**	**0.0056**	**<0.0001**
Type 2	0.3069		**0.007**	0.3072	0.2079	**<0.0001**
Type 3	**<0.0001**	**0.007**		0.161	0.3489	**<0.0001**
Type 4	**0.0063**	0.3072	0.161		0.7749	**0.0004**
Type 5	**0.0056**	0.2079	0.3489	0.7749		**0.0016**
Type 6	**<0.0001**	**0.0004**	**<0.0001**	**0.0004**	**0.0016**	
PC2	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Type 1		**0.0062**	**<0.0001**	0.1467	**<0.0001**	**0.0247**
Type 2	**0.0062**		**0.026**	0.6985	0.1934	0.5623
Type 3	**<0.0001**	**0.026**		**0.0155**	0.7549	**0.0002**
Type 4	0.1467	0.6985	**0.0155**		0.1405	0.9259
Type 5	**<0.0001**	0.1934	0.7549	0.1405		0.0801
Type 6	**0.0247**	0.5623	**0.0002**	0.9259	0.0801	
PC3	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Type 1		0.7334	**0.0292**	0.0517	**0.0009**	0.8258
Type 2	0.7334		0.4259	0.2453	**0.0098**	0.8167
Type 3	**0.0292**	0.4259		0.7006	**<0.0001**	0.1281
Type 4	0.0517	0.2453	0.7006		**0.0004**	0.2265
Type 5	**0.0009**	**0.0098**	**<0.0001**	**0.0004**		**0.0011**
Type 6	0.8258	0.8167	0.1281	0.2265	**0.0011**	
PC4	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Type 1		**0.004**	0.9626	0.7187	0.316	0.1033
Type 2	**0.004**		**0.0034**	**0.0067**	**0.001**	0.132
Type 3	0.9626	**0.0034**		0.7006	0.2589	0.0831
Type 4	0.7187	**0.0067**	0.7006		0.6129	0.0507
Type 5	0.316	**0.001**	0.2589	0.6129		**0.0158**
Type 6	0.1033	0.132	0.0831	0.0507	**0.0158**	

Table 6.5: p-values of Mann-Whitney pairwise comparisons of a Kruskal-Wallis test for PC1 to PC4 of the between groups PCA on all extant phalanges, with significant values ($p<0.05$) in bold.

Type 5 specimens (cursorial/wet environment) also overlapped substantially with the other groups, but not to the same extent as the type 4 group. In the scatterplot the type 5 group appeared to be more similar in score to the type 3 specimens. This pattern was confirmed by the pairwise comparisons associated with the Kruskal-Wallis test (Table 6.5). Type 5 specimens were significantly different from type 1 specimens (p=0.005676) and type 6 specimens (p=0.001632), but not from the type 2 (p=0.2079), type 3 (p=0.3489) and type 4 specimens (p=0.7749). This would be in line with the functional hypotheses, as both groups

are found in environments with a more yielding substrate, which would be associated with an increased capacity for splaying the phalanges.

Type 6 specimens (tundra/cursorial) formed a somewhat unusual group and gave the most negative scores on the first axis. This implied that the intermediate phalanx in reindeer had a more gracile shape than that of the wet adapted species. As expected, this was confirmed by the pairwise comparisons associated with the Kruskal-Wallis test (Table 6.5). Differences between the type 6 group and the type 1 (p<0.0001), type 2 (p=0.0004091), type 3 (p<0.0001), type 4 (p=0.0004584) and type 5 groups (p=0.001632) were all highly significant. This observation confirmed the suspicion that the morphology of the reindeer phalanges is different from that of all other cervid species.

PC2 was responsible for 37.9% of the total variance. Two major shape differences were observed in the thin plate spline deformation grids associated with this component (Fig. 6.16). A first shape change along this axis was a difference in the size of the distal articulation and in the height of the extensor process on the anterior side of the distal articulation. Specimens with a lower score had smaller shaped distal articulations relative to the rest of the element and an extensor process positioned lower on the anterior side of the phalanx. Specimens with a higher score had a larger distal articulation relative to the rest of the phalanx and an extensor process positioned higher on the anterior side of the phalanx.

A second shape change that was observed (Fig. 6.16), was a difference in morphology of the proximal articular surface. In specimens with a low score the proximal articulation was deeper and more concave in shape. Specimens with a higher score had a flatter and less deep proximal articular surface. Part of these shape changes seem to be linked to some of the functional hypotheses that were proposed for this element. The height of the extensor process is thought to be further extended in more cursioral, open habitat species because it increases

the flexibility of the terminal phalanx in the sagittal plain and allows for a higher capacity to withstand forces when running and increases the "pogostick effect" (Leinders 1979).

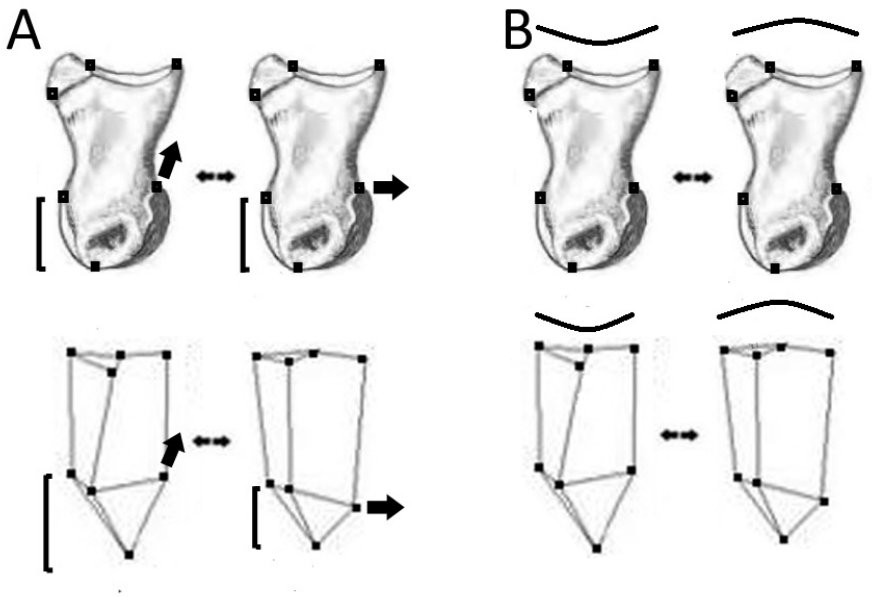


*Figure 6.16: Shape changes observed along the axis of PC2 of a bg-PCA on all extant phalanges, with visualizations all from medial perspective. The illustrations on the bottom present landmark configurations registered on the calcaneus, the illustrations at the top; their corresponding positions on the bone. In "**A**" a difference in size of the distal articulation and difference in placement of the extensor process on the anterior side is shown. Specimens with a low score on PC2 (bottom far left) had a long distal articular surface relative to the size of the phalanx and a highly placed extensor process on the anterior side. Specimens with a high score on PC2 (bottom, second from the left) had a small distal articular surface relative to the size of the phalanx and a low extensor process on the anterior side. In "**B**" a difference in depth of the proximal articular surface is shown. Specimens with a low score on PC2 (bottom, second from the right) had a relatively deep, concave proximal articular surface. Specimens with a high score on PC2 (bottom, first from the right) had a flatter, more shallow proximal articular surface.*

It is therefore likely that this shape difference represents a functional signal. Similarly, the shape of the proximal articular surface was also mentioned in the proposed functional hypotheses. A more concave proximal articular surface was predicted to be more commonly found in cursorial animals, associated with more open environments. Köhler (1993) linked the deep articular surface to a reduction in medio-lateral movement of the articulation, which would prevent the interphalangeal joint from disarticulating during fast running. This shape

difference is probably at least in part functional. The relative size of the distal articulation was not predicted in any of our functional hypotheses. It is unclear whether this variation in shape was also driven by functional differences.

An assessment of the scatterplots associated with the second component suggested that the patterns observed in the thin plate spline deformation grids and the proposed functional hypotheses were at least partially confirmed (Fig. 6.14 and 6.17). Visual overlap between the groups was substantial, but certain patterns could still be discerned (see following paragraph), especially when PC2 was plotted against PC1 (Fig. 6.14). When PC2 was plotted against PC3 (Fig. 6.17) there was more visual overlap, as expected, and separations were mainly driven by the second component.

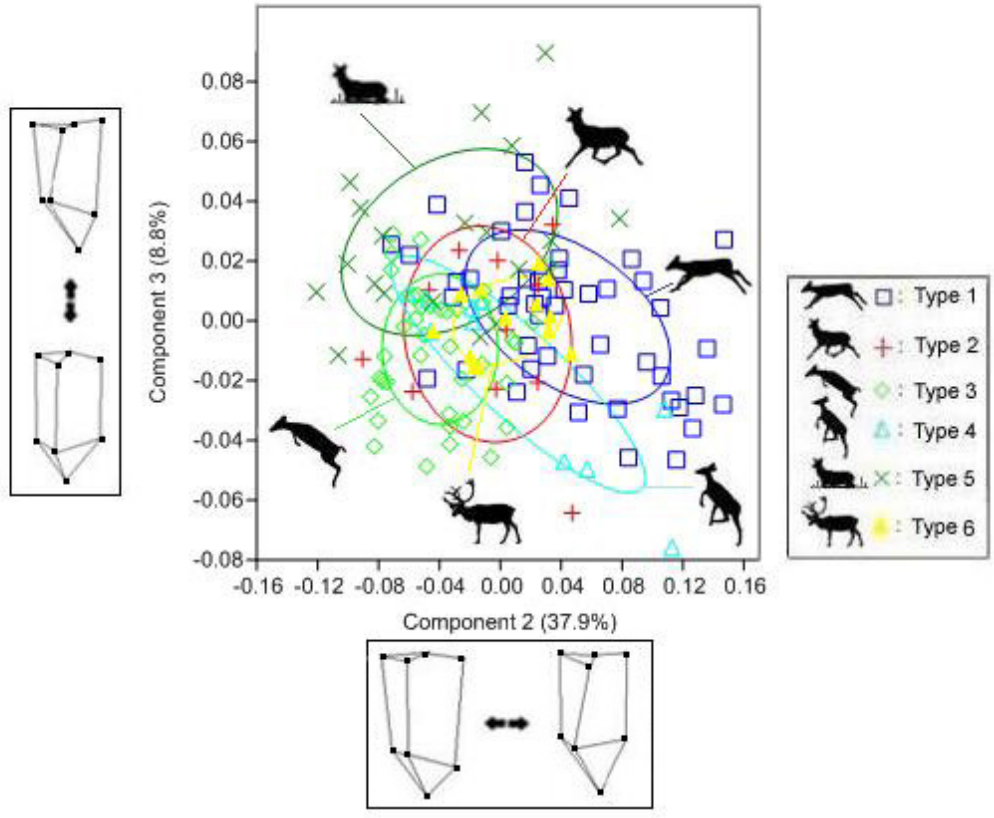


Figure 6.17: PC2 and PC3 scatterplot of a between groups PCA of all extant phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.

Similar to the first axis, type 1 specimens (cursorial/open/dry substrate) gave higher scores on PC2 than the type 3 group (saltatorial/closed/wet substrate), while the group of type 2 specimens gave an intermediate score (Fig. 6.14 and 6.17). This suggested a gradient between type 1, 2 and 3 specimens that was also observed along the first axis, related to functional differences. The Kruskal-Wallis test (Table 6.5) confirmed the significance of between group differences (H=50.95, p<0.0001). Pairwise comparisons indicated significant differences on this axis between type 1 and type 2 specimens (p=0.006248), between type 1 and type 3 specimens (p<0.001) and type 2 and 3 (p=0.02609) (Table 6.5). These results implied that all groups generally had a substantially different shape, but that intermediate type 2 specimens were perhaps more similar in shape to saltatorial type 3 specimens, associated with wet, closed environments along this axis.

Type 4 specimens, associated with mountainous habitats, behaved similar on PC2 as on PC1 (Fig. 6.14 and 6.17). Specimens tended to be dispersed on the scatterplot. This resulted in the pairwise comparisons (Table 6.5) in no significant differences from the type 1 (p=0.1467), type 2 (p=0.6985), type 5 (p=0.1405) and type 6 groups (p=0.9259). The type 4 group was, however, indicated to be more different from the type 3 group (saltatorial/closed/wet) (p=0.1558) on this axis. Contrary to the observed between-group relationships along the first component, this could suggest that the high altitude type 4 species had a morphology more similar to that of animals of cursorial behaviour, found in more open/dry environments.

Similarly, type 5 specimens, found in open wetland environments and associated with a somewhat more cursorial escape strategy, displayed substantial overlap with the other groups on the second axis (Fig. 6.14 and 6.17). This group visually gave a similar score to the type 3 specimens associated with a saltatorial behaviour and closed, relatively wet environments and with the intermediate type 2 group. In the pairwise comparisons (Table 6.5) these differences

were only confirmed to the extent that the type 5 group was significantly different on this axis from the type 1 group (p<0.001), associated with cursoriality and open, relatively dry environments. No significant differences were found between this group and the type 2 (p=0.1934), type 3 (p=0.7549), type 4 (p=0.1405) and type 6 specimens (p=0.0801). The highest p-values were however measured for the type 3 group, perhaps indicating type 5 specimens were most similar to the latter. These results could imply that the phalanges in the type 5 group had a morphology associated with an increased capacity for splaying as was predicted in the functional hypotheses. In the calcaneus analysis this group appeared to be morphologically more similar to the cursorial type 1 specimens, a result that at first sight contradicts with that of the phalanges. But, it is not unlikely that the shape of the phalanges is more driven by substrate type than the calcaneus. This could be interpreted as characteristic for open wetland species, with calcanei adapted for cursorial movement in open landscapes, but with phalanges suitable for more yielding substrates.

Type 6 specimens were not well separated on the second axis of the PCA. Although this group of specimens was well separated on the first axis, on PC2 the type 6 specimens gave intermediate results that plotted out similar to the type 2 specimens. This was reflected in the results of the pairwise comparisons following the Kruskal-Wallis test (Table 6.5). The type 6 specimens were not significantly different on this axis from the type 2 (p=0.5623), type 4 (p=0.9259) and type 5 groups (p=0.0801). Significant differences were, however, found between the type 6 groups and the type 1 (cursorial/open/dry substrate) (p=0.02474) and type 3 groups (saltatorial/closed/wet substrate) (p<0.001). This result indicated that although the relative gracility of the reindeer phalanges is higher than in most other species (see PC1), the shape variation in the proximal and distal articulation, that were expected to be driven by functional differences related to locomotion and vegetation/substrate type, are not observed in this group.

PC3 was responsible for 8.8% of the total variance in the dataset. Two main shape differences were noted along this axis (Fig. 6.18). A first shape difference was similar to one of those already observed along PC2. A variation was noted in depth and concavity of the proximal articular surface. Specimens with a higher score had a deeper, more concave proximal articular surface, while in specimens with a lower score the proximal articular surface was flatter and shallower. Similar to PC2, this shape difference can probably also be interpreted as the one that was described in the functional hypotheses. A deeper articular surface was hypothesized to provide more joint stability during fast running in cursorial forms (Köhler 1993).

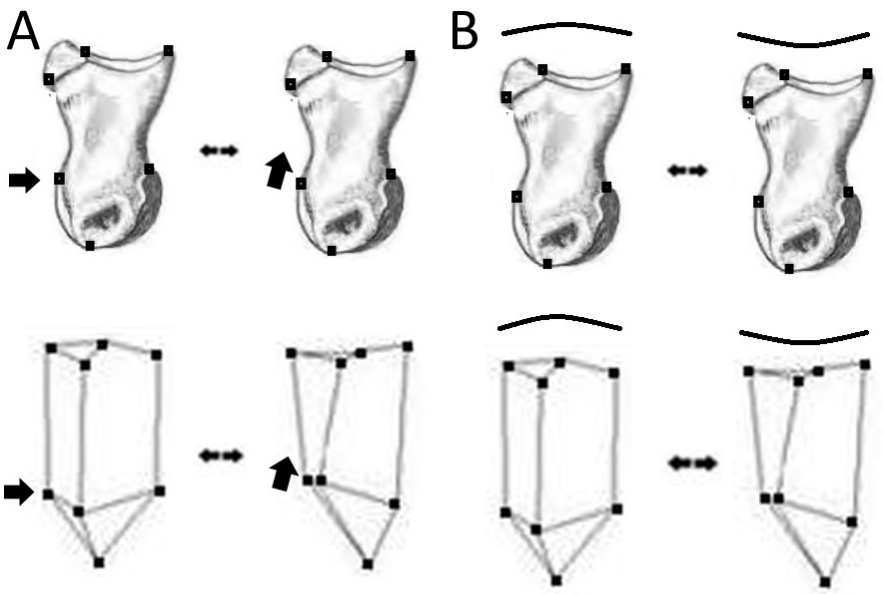


*Figure 6.18: Shape changes observed along the axis of PC3 of a between groups PCA on all extant phalanges, with visualizations all from medial perspective. The illustrations on the bottom present landmark configurations registered on the intermediate phalanx, the illustrations at the top; their corresponding positions on the bone. In "**A**" a difference in height of the palmar extensions on the posterior side of the distal articulation is shown. In specimens with a low score on PC3 (bottom, first from the left) the palmar extensions on the posterior side were relatively low. In specimens with a high score on PC3 (bottom, second from the left), the palmar extensions on the posterior side were relatively high. In "**B**" a difference in the shape of the proximal articular surface is shown. In specimens with a low score on PC3 (bottom, second from the right) the proximal articular surface was relatively flat and less deep. In specimens with a high score on PC3 (bottom, first from the right) the proximal articular surface was deeper and more concave.*

A second shape change that appeared to be summarized by the third axis was a difference in height of the palmar extensions on the posterior side of the distal articular surface. The palmar extentions were found to extend further to the proximal side in specimens with a more positive score and were found at a lower height in specimens with a negative score. This variation in shape was also predicted in our functional hypotheses and may be similarly explained as the height of the anterior extensor process. Cursorial species found in more open environments were predicted to have higher palmar extensions as they increase flexibility of the terminal phalanx and amplify the "pogostick effect" and allow animals to withstand higher forces when zig-zag running at high speed (Leinders 1979). It seems likely that the concavity of the proximal articular surface and the height of the palmar extensions to some extent signal a functional difference.

Assessment of the scatterplots associated with the third component revealed less clear patterns that could be associated with the proposed functional hypotheses (Fig. 6.17 and 6.19). There was much more visual overlap between the groups than on the first two axes, so that few clusters could be clearly discerned. Only the type 5 group was somewhat separated from the other groups, but this was mainly clear when PC3 was plotted against PC2 and, in that case, the separation was also driven by the latter component (Fig. 6.17). When PC3 was plotted against PC4 (Fig. 6.19) visual separations became even more minimal.

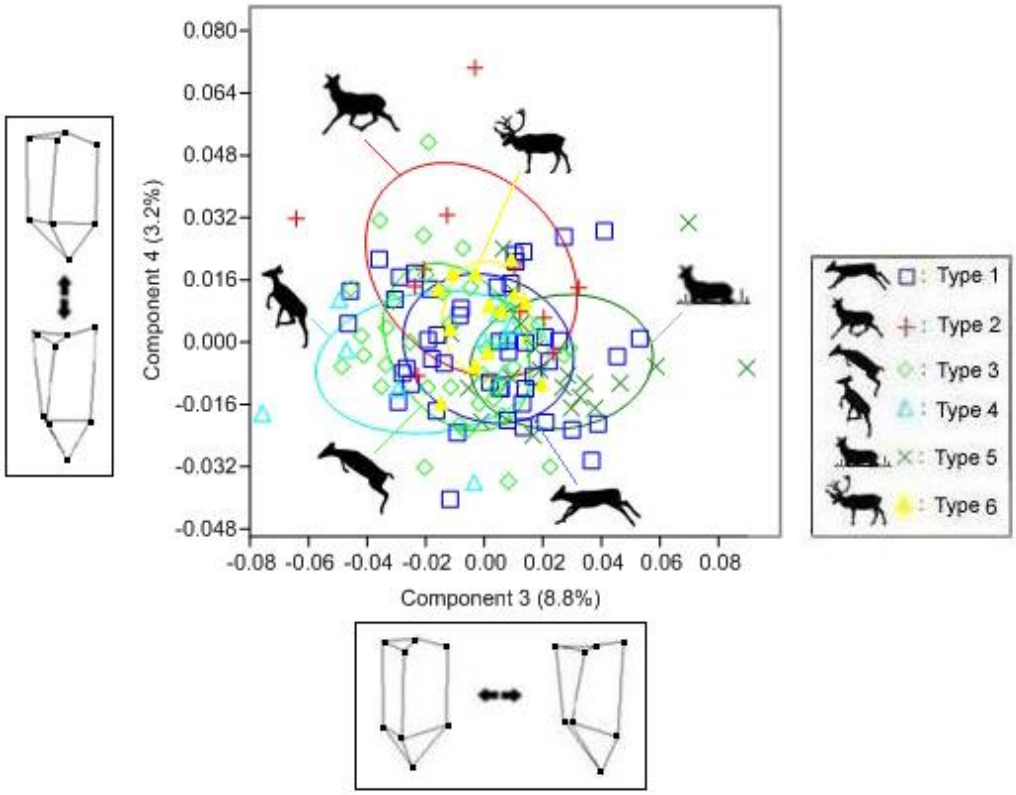


Figure 6.19: PC3 and PC4 scatterplot of a between groups PCA of all extant phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.

Although few differences were discerned visually, group separations were nevertheless found to be significant by the Kruskal-Wallis test (H=27.69, p<0.0001). Pairwise comparisons (Table 6.5), moreover, indicated that the type 5 specimens were significantly different from type 1 (p=0.0009073), type 2 (p=0.009869), type 3 (p<0.0001), type 4 (p=0.0004696) and type 6 specimens (p=0.001111), confirming the visual separation of this cluster. In addition, the group of type 1 specimens was also significantly different from the type 3 specimens (p=0.02921). Although the latter two groups were visually not well separated, they were expected to be functionally most different from each other. As the shape changes explained by this axis were predicted in the proposed functional hypotheses, it not unlikely that the third

component is to some extent picking up a functional signal, but given the large overlap this signal is perhaps less strong as in first two components.

PC4 explained only 3.2% of the total variation in the dataset. The shape differences observed along this axis visually appear to be similar to those differences already described for the other components (Fig. 6.20). The fourth component also describes a difference in overall gracility of the element, but in this case alongside other shape changes. Specimens with a higher score had more robust phalanges than specimens with a lower score. How the shape variation explained by this axis is related to that of the first component is unclear. Like in the first component, variation in gracility of the phalanges is probably explained in part by functional differences. Unlike the morphological variation described by PC1, in PC4 differences in gracility seem to be mainly expressed in the shaft and proximal articulation. The distal articulation does not seem to increase as much in size, giving the elements with a higher score on this axis an "inflated" look. Furthermore, this component also seems to express variation in the depth of the proximal articular surface, a shape difference similar to that described by PC2 and PC3. Along the fourth axis, specimens with a lower score had deeper, more concave proximal articular surfaces. In specimens with a high score, the proximal articular surface was less deep. Judging from the deformation grids, it is possible that the shape changes observed along PC4 are at least in part functional.

Assessment of the scatterplot associated with PC4 (Fig. 6.19) revealed little visual separation between the groups. Most specimens clustered together in the center of the graph. Only the type 2 group (intermediate specimens) was visually separated from the main cluster when plotted against PC3. Other separations were driven by PC3. This was confirmed by the results of the Kruskal-Wallis test indicating significant between group differences (H=16.17, p=0.0063). Pairwise comparisons showed significant differences between the type 2 group

and the type 1 (p=0.004095), type 3 (p=0.003418), type 4 (p=0.006706) and type 5 group (p=0.00103) (Table 6.5). Differences with the type 6 group were non-significant (p=0.132). Although not visually clear in the scatterplot, type 5 specimens were also considered significantly different from type 6 specimens (p=0.01581). Although the deformation grids may indicate a potential connection with the proposed functional hypotheses, the weak separations associated with this shape variable do not support a strong functional signal along this axis.

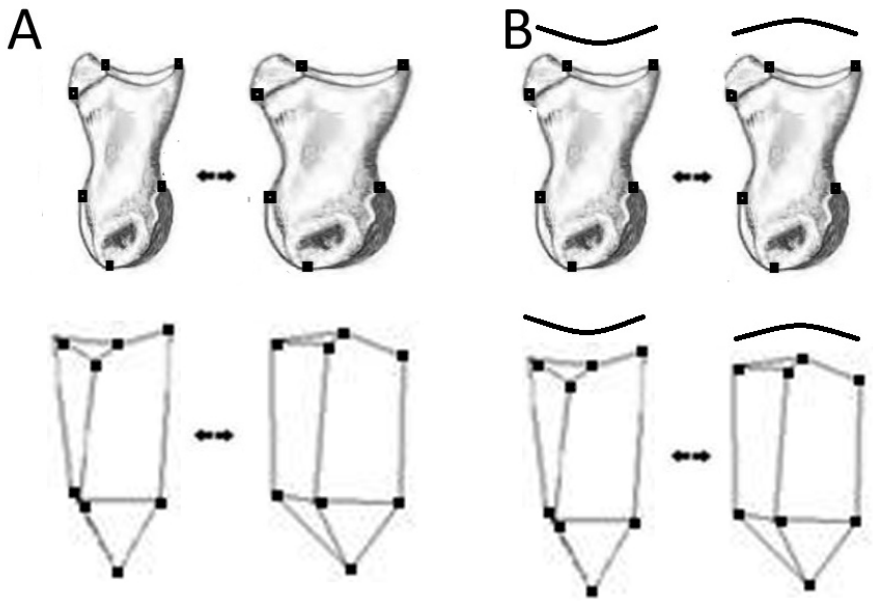


*Figure 6.20: Shape changes observed along the axis of PC4 of a between groups PCA on all extant phalanges, with visualizations all from medial perspective. The illustrations on the bottom present landmark configurations registered on the intermediate phalanx, the illustrations at the top; their corresponding positions on the bone. In "**A**" a difference in gracility of the phalanx is shown. Specimens with a low score on PC4 (bottom, far left) had a more gracile shaft and proximal articulation. Specimens with a high score on PC4 (bottom, second from the left) had a more robust shaft and proximal articulation. In "**B**" a difference in the shape of the proximal articular surface is shown. Specimens with a low score on PC4 (bottom, second from the right) had a more concave proximal articular surface. Specimens with a higher score on PC4 (bottom, far right) had a flatter, more shallow proximal articular surface.*

Allometry

The results of an ordinary least squares regression of the shape variables against log centroid size suggested that to some extent an allometric effect was present in the morphometric dataset. Fitted line plots associated with the regressions are provided in Appendix H. A regression of PC1 against log centroid size indicated a significant, although very weak correlation between size and this shape variable (R^2=0.0629, p=0.0026). This implied that only a small portion of the shape variance explained by PC2 could be attributed to the allometric effects of size differences. A somewhat larger allometric effect was suggested by the results of a regression of the second component against log centroid size (R^2=0.2579, p<0.001). Although in this component a larger portion of the shape variance could be attributed to size differences, overall this was still relatively limited and probably only partially explained measured shape differences. When PC3 was regressed against centroid size, the results indicated a significant, but limited correlation (R^2=0.0276, p=0.0488). As in PC1, this suggested that the allometric effects of size differences played only a minor role in the shape differences explained by this axis. The regression of PC4 against centroid size did not reveal a significant correlation between shape and size (R^2=0.0199, p=0.0946), implying that the allometric effects of size difference had little to no effect on this component.

Phylogeny

A phylogenetic generalized least squares regression of the relevant principal components (PC1 to PC4) against habitat/locomotor dummy variables indicated that phylogeny may have an effect on the shape differences summarized by the PCA (see full output data and R-scripts in Appendix I). The PGLS regression resulted in a high pagel's λ (0.811) that was not significantly different from 1 ($p(H_0:\lambda=1)$=0.0667) or from 0 ($p(H_0:\lambda=1)$=0.0725). From these results it could be interpreted that there was a phylogenetic signal in the dataset, but given that

p-values were not significantly different from the upper (1) and lower bound (0), it was likely that phylogenetic relatedness was only partially responsible for the morphological differences summarized by the PCA.

A re-assessment of PCA scatterplots after calculating the mean shapes per species generally confirmed the results from the PGLS regression. While some closely related taxa appeared to cluster together as a result of phylogenetic relatedness, no clear patterns were observed that would suggest that phylogeny was the predominant driver of shape differences in the dataset (Fig. 6.21, 6.22, 6.23 and 6.24). Phylogeny did, however, most likely contribute to certain separations.

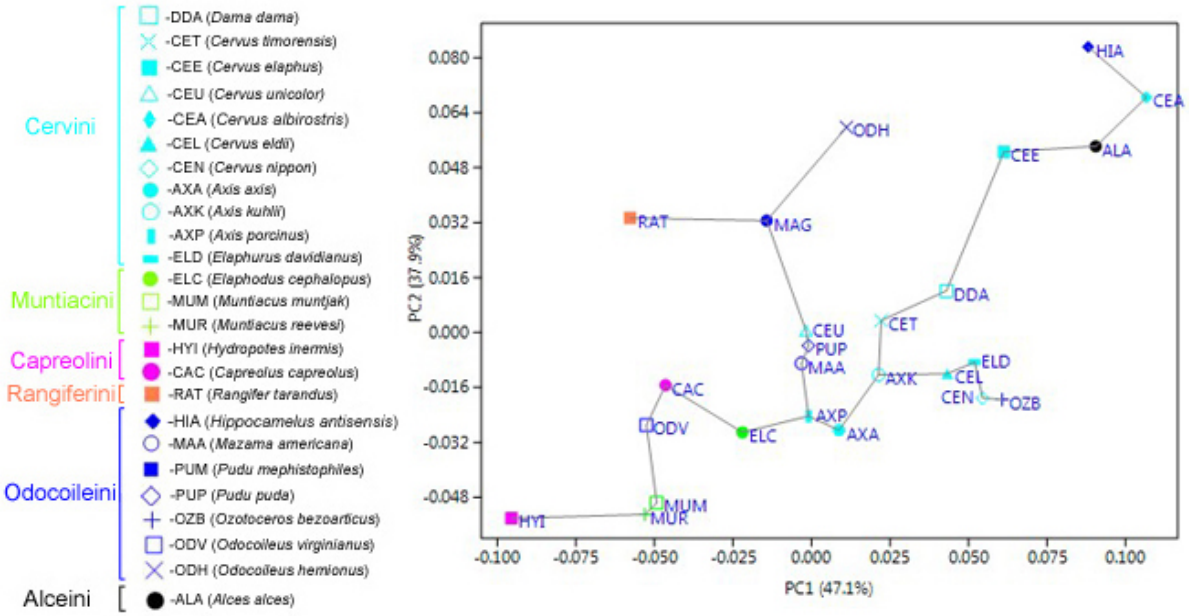


Figure 6.21: Scatterplot of mean shapes per species as described by PC1 and PC2 of a bg-PCA on all phalanx specimens with minimal spanning tree representing shortest possible distance between data points.

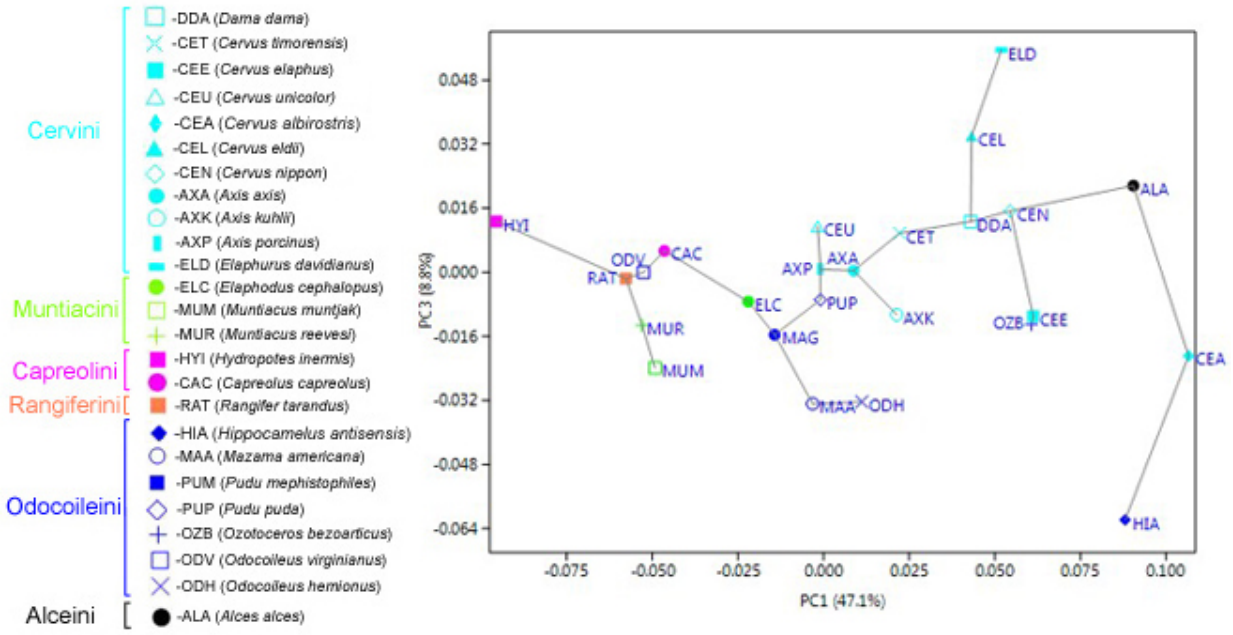


Figure 6.22: Scatterplot of mean shapes per species as described by PC1 and PC3 of a bg-PCA on all phalanx specimens with minimal spanning tree representing shortest possible distance between data points.

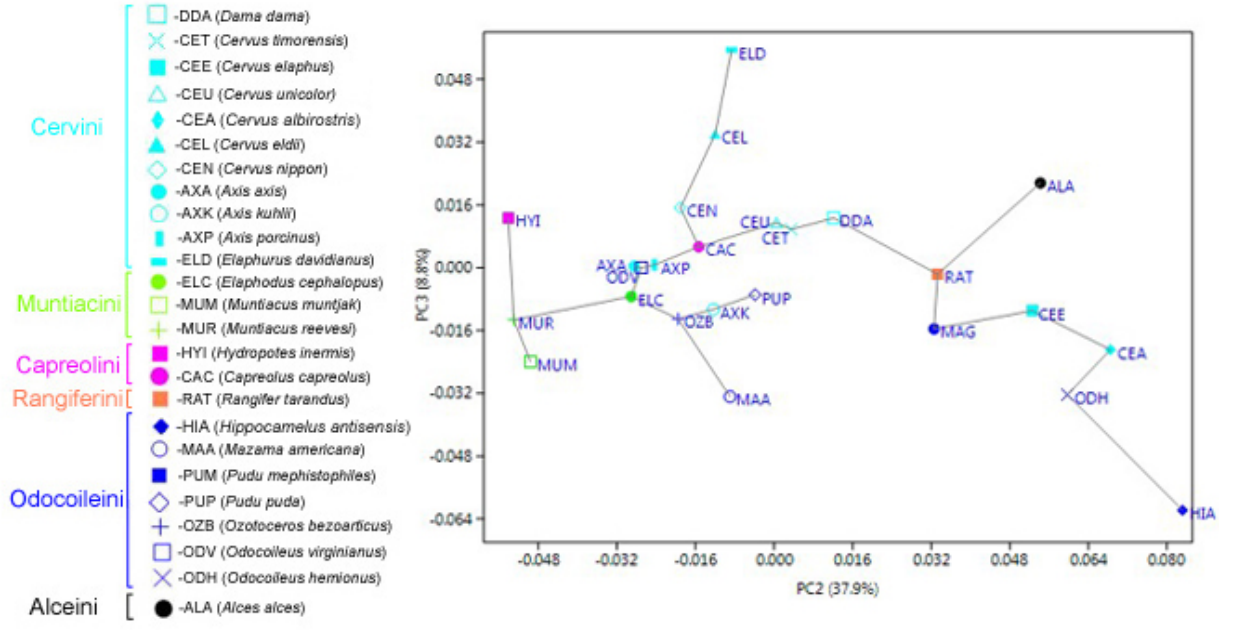


Figure 6.23: Scatterplot of mean shapes per species as described by PC2 and PC3 of a bg-PCA on all phalanx specimens with minimal spanning tree representing shortest possible distance between data points.

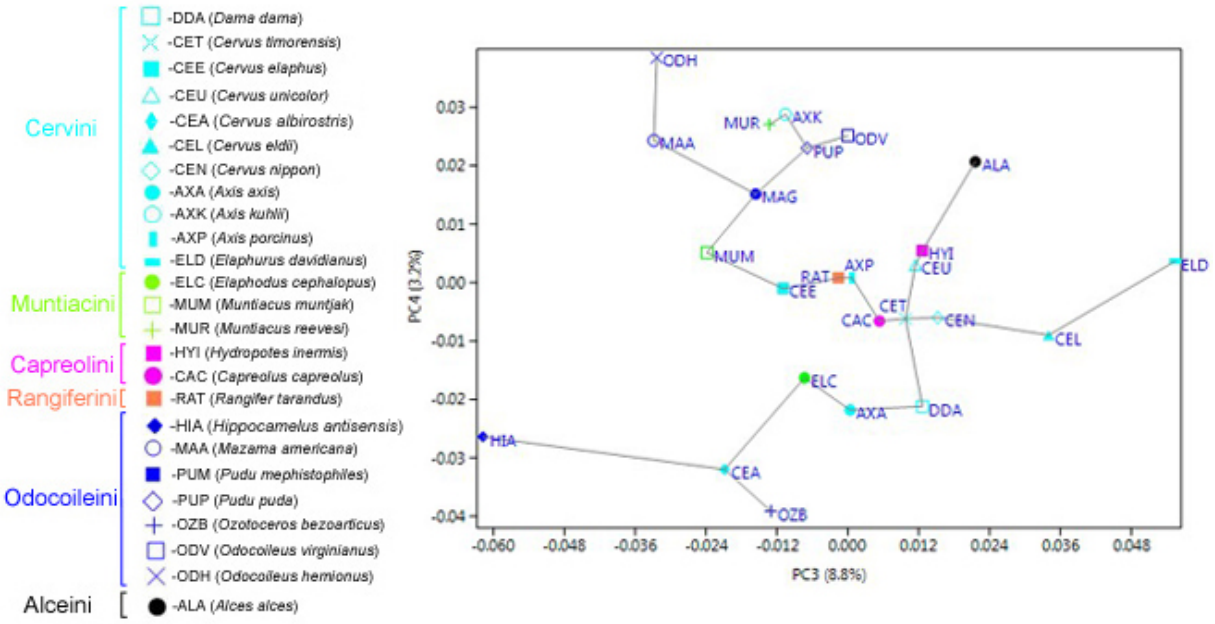


Figure 6.24: Scatterplot of mean shapes per species as described by PC3 and PC4 of a bg-PCA on all phalanx specimens with minimal spanning tree representing shortest possible distance between data points.

On PC1 most members of the Cervini tribe gave a relatively high score (Fig. 6.21 and 6.22). In addition, members of the same genus or subgenus within this tribe, such as the *Axis* deer and the subgenus *Rusa* were found in close proximity to each other when PC1 was plotted against PC2 or PC3 (Fig. 6.22 and 6.22). Especially for the genus *Axis* this could well be the result of phylogenetic relatedness, as the species within this group do not occupy very similar habitats. However, several other species outside of the Cervini tribe (e.g. *Hippocamelus antisensis*, *Ozotoceros bezoarticus* and *Alces alces*) had a similarly high score on the first axis that cannot be explained by phylogenetic relatedness only. In addition, it is interesting to note that within the group of Cervini, the species associated with a more cursorial behaviour or with a more open habitat preference (e.g. *Cervus albirostris* and *Dama dama*) often had a higher score than those species associated with a more closed habitat preference and saltatorial behaviour (e.g *Cervus unicolor*). On the second axis the Cervini did not give similarly high scores as on PC1 and the pattern described for the first component seemed to

be confounded by a number of unrelated species (e.g. *Rangifer tarandus* and *Odocoileus hemionus*) giving similar scores on the axis as the Cervini species (Fig. 6.21 and 6.23). *Cervus elaphus* and *Cervus albirostris* gave a very high score on PC2. Especially when PC2 was plotted against PC1 these species clustered closely together. While these forms are closely related, it is worth mentioning that *Cervus nippon*, which forms a sister taxon with *Cervus albirostris* and *Cervus elaphus*, does not behave in the same way and gave a lower score, more similar to e.g. *Elaphurus davidianus*. This would suggest other factors besides phylogeny driving shape differences. PC3 (Fig. 6.22, 6.23 and 6.24) and PC4 (Fig. 6.24) did not reveal any clear patterns for this tribe that could be associated with phylogenetic relatedness.

The placement of the Muntiacini tribe along the PCA scatterplots suggested that its shape was in part driven by phylogenetic relatedness. The members of this group consistently clustered together when PC1 was plotted against PC2 (Fig. 6.21), when PC1 was plotted against PC3 (Fig. 6.22) and when PC2 was plotted against PC3 (Fig. 6.23). On the first three components the group always gave rather negative scores. This was especially the case for the two species of the genus *Muntiacus*, but also the third species in this group (*Elaphodus cephalopus*) was often found in close proximity to the muntjacs. Although it is likely that phylogeny played a role here, it should be mentioned that the muntjacs have a similar habitat preference and that the unrelated *Hydropotes inermis* also had the tendency to cluster closely together with the muntjacs. It is therefore likely that the shape of the phalanges in this tribe is also driven by a combination of functional and phylogenetic factors. This could perhaps indicate that larger patterns in the scatterplots corresponded to differences between locomotor/functional groups, but that variation within these groups is to a certain extent driven by phylogeny.

The Odocoileini did not appear to follow the patterns observed for the Cervini and Muntiacini and separations did not seem to be driven at all by phylogeny in this group. As opposed to the

Cervini and the Muntiacini, the members of the Odocoileini tribe were spread over the scatterplots of all axis combinations (Fig. 6.21, 6.22, 6.23 and 6.24). Moreover, when considering PC1 (Fig. 6.21 and 6.22), the species in this tribe that were associated with more open habitats or a more cursorial strategy (e.g. *Ozotoceros bezoarticus*) tended to give higher scores than those associated with closed habitats and saltatorial behaviour (e.g. the genus *Mazama*). For PC2, PC3 and PC4 (Fig. 6.21, 6.22, 6.23 and 6.24) this division was less clear, but the position of this group along these axes gave similar results and tended to support a functional explanation.

The Rangiferini gave a rather negative score on PC1, similar to the type 3 group (including *Hydropotes* and *Muntiacus*) (Fig. 6.21 and 6.22), but high scores on PC2, more similar to the type 1 and type 2 groups (Fig. 6.21 and 6.23). When the first two axes were plotted together, the species closest to the Rangiferini on the scatterplot were *Mazama gouazoupira* and *Odocoileus hemionus*, members of the Odocoileini tribe. As the Odocoileini tribe is closely related to the Rangiferini tribe, it is possible that the clustering of these species is to a certain extent driven by phylogenetic relatedness. However, the distance between *Rangifer* and these other species is still large. Moreover, the Rangiferini group was well separated on its own and had a very peculiar placement on the scatterplot of all specimens (see Fig. 6.14 and 6.15). It is therefore likely that functional differences played a large role in driving separations on the scatterplots of the first two components (Fig. 6.21, 6.22 and 6.23). As allometry played a limited role on the second axis, it may be that size differences also drove specimen distribution to some extent on PC2. On PC3 and PC4 the Rangiferini gave more intermediate scores. When PC2 was plotted against PC3 (Fig. 6.23) this led to *Alces alces* and *Mazama gouazoupira* being the two closest species. *Alces* and *Mazama* are both relatively closely related to the Rangiferini tribe, so phylogeny may have played a role here. When PC3 was

plotted against PC4 no meaningful relationships were discerned from visual assessment of the scatterplot (Fig. 6.24).

The Alceini tribe, consisting of *Alces alces* only, is most closely related to the Rangiferini and Odocoileini tribes. The placement of the *Alces* specimens on the scatterplots did not necessarily result in a clustering with these two tribes. On the first two axes (Fig. 6.21, 6.22 and 6.23) *Alces* gave very high scores, similar to some of the type 1 Cervini (e.g. *Cervus elaphus*), but also to the more closely related *Hippocamelus antisensis*. As the other Odocoileini specimens were spread all over the scatterplots and did not indicate that phylogeny played a substantial role in their distribution, its closeness to *Alces* should therefore not necessarily be considered phylogenetically meaningful. On PC3 *Alces* gave more intermediate scores (Fig. 6.22, 6.23 and 6.24). When PC3 was plotted against PC2 (Fig. 6.23), *Rangifer tarandus* was the closest species to *Alces* on the scatterplot. As the Rangiferini tribe is relatively closely related to the Alceini tribe, phylogeny may have played a role here. When PC3 was plotted against PC4 (Fig. 6.24), *Alces* was closest to *Hydropotes inermis*. There were no patterns observed on the scatterplot that would indicate that specimen placement on the fourth axis was primarily driven by phylogeny here.

The members of the Capreolini tribe (*Hydropotes inermis* and *Capreolus capreolus*) gave low scores on the first two axes (Fig. 6.21, 6.22 and 6.23), but the two species never clustered particularly close together. Other, not closely related, species such as *Muntiacus muntjak* and *Muntiacus reevesi* gave similar scores on PC1 and PC2 (Fig 6.21, 6.22 and 6.23). On PC3 and PC4 the scores for these species were more intermediate (Fig 6.22, 6.23 and 6.24). When PC3 was plotted against PC2 (Fig. 6.23) *Hydropotes inermis* was closest to the Muntjacs again, but *Capreolus capreolus* closer to some of the Cervini such as *Cervus nippon* and the *Axis* deer. When PC3 was plotted against PC4, the Capreolini were close to some of the Cervini again,

in particular species such as *Cervus unicolor* and *Cervus timorensis*. It would appear that phylogenetic relatedness played only a limited role in driving the position of specimens in this tribe on the PCA scatterplots. Especially on the first two axes, separations appear to be more driven by functional differences.

In sum, the results of the PCA and the regressions suggested that the morphological variation described by the first three principal components was driven by a combination of function and phylogeny. The fourth component did not appear to describe meaningful ecological or phylogenetic patterns. Allometry seemed to play a minor role as a confounding factor in the dataset, although its effects may be felt to some extent on the second component. This effect was nevertheless considered limited. The major patterns observed in the scatterplots appeared to correspond primarily to differences in habitat and/or locomotor behaviour. On a smaller scale, certain closely related taxa had a tendency to cluster together, mainly within these larger (functional/ecological) groups. Similar to the results of the calcaneus model, a scenario where each shape component was driven by a closely intertwined combination of functional and phylogenetic factors was considered most realistic. That being said, on the first two components, the functional signal was probably the strongest, as separations between habitat/locomotor groups were more pronounced and because the shape variations explained by these axes corresponded well to the morphological differences that were predicted in the functional hypotheses.

6.3 Results fossil specimens

6.3.1 Trinil and *Axis lydekkeri*

6.3.1.1 Introduction

For the analysis of the Trinil specimens a combination of intermediate phalanges and calcanei were used. In total 15 purported *Axis lydekkeri* phalanges from this site were added to the extant species model, that together added up to a combined dataset of 157 specimens. Furthermore, 28 fossil calcanei, also identified as *Axis lydekkeri*, were added to the calcaneus model, amounting to a combined dataset of 153 specimens (see Tables 5.2 and 5.3).

In addition a small number of extra *Axis lydekkeri* fossils were added to the Trinil datasets in order to assess the locomotor strategy and habitat preference of this species as a unit of analysis. The additional fossils (three calcanei and six phalanges) came from non-specified Pleistocene localities in East/Central Java and resulted in two datasets of respectively 156 (calcanei) and 163 (phalanges) specimens (see Tables 5.2 and 5.3).

In each combined dataset the appended files were re-submitted to a new GPA, after which a bg-PCA was run on the procrustes residuals. An NPMANOVA was conducted on the relevant principal components and scatterplots were provided for those components that were deemed significant for the ecomorphological analysis (see section 6.2). The Kruskal-Wallis test was used to assess significance of between group differences along individual axes. Eigenvalues and broken stick distributions associated with the PCA were provided in Appendices J (calcaneus) and K (intermediate phalanx).

6.3.1.2 Calcaneus

The results of an NPMANOVA on PC1 to PC4 of the PCA-scores on the Trinil specimens indicated significant between group differences (F=9.16, p=0.0001). Pairwise comparisons

(Table 6.6-A) revealed the same differences between the habitat/locomotion groups as discussed in the results of the extant species model (section 6.2.1.3). Only the difference between the type 2 and type 3 groups was not significant in multidimensional space (p=0.2472). This indicated that adding the fossil sample to the extant dataset did not interfere to a large extent with the patterns observed in the model. The sample from Trinil was significantly different from most habitat/locomotion groups. Differences from the type 3 group (p=0.0001), the type 2 group (p=0.0001) and the type 5 group (p=0.0001) were highly significant, and significant differences (p=0.0173) were also measured between the Trinil fossils and the type 1 group. No significant differences were, however, found between the type 4 group and the Trinil sample (p=0.1953).

Adding the additional *Axis lydekkeri* specimens to the sample did not alter most of the patterns described in the more restricted Trinil dataset (Table 6.6-B). Similar to the analysis of the Trinil specimens, the NPMANOVA indicated significant between group differences (F=9.64, p=0.0001). In the pairwise comparisons significant differences were measured between most extant groups, with the exception of the type 2 and type 3 groups (p=0.2035). The *Axis lydekkeri* specimens themselves were significantly different from the type 1 group (p=0.0135) and highly significantly different from the type 3 (p<0.001), type 2 (p<0.001) and type 5 groups (p<0.001). No significant difference was measured between the *Axis lydekkeri* specimens and the type 4 group (p=0.1243).

The pairwise comparisons in other words indicated that the specimens from Trinil, as well as the unprovenanced *Axis lydekkeri* specimens, were morphologically most similar to extant forms found in mountainous environments and perhaps to some extent to the cursorial type 1 forms, found in more open environments. The analysis also indicated that the specimens from Trinil were different in morphology from saltatorial species found in closed environments and from forms associated with open, wet environments.

A (TRIN)	Type 3	Type 2	Type 4	Type 1	TRIN	Type 5
Type 3	-	0.2472	**0.003**	**0.0001**	**0.0001**	**0.0001**
Type 2	0.2472	-	**0.0211**	**0.0034**	**0.0001**	**0.0019**
Type 4	**0.003**	**0.0211**	-	**0.0071**	0.1953	**0.0001**
Type 1	**0.0001**	**0.0034**	**0.0071**	-	**0.0173**	**0.0001**
TRIN	**0.0001**	**0.0001**	0.1953	**0.0173**	-	**0.0001**
Type 5	**0.0001**	**0.0019**	**0.0001**	**0.0001**	**0.0001**	-

B (ALY)	Type 3	Type 2	Type 4	Type 1	ALY	Type 5
Type 3	-	0.2035	**0.0032**	**0.0001**	**0.0001**	**0.0001**
Type 2	0.2035	-	**0.0188**	**0.002**	**0.0001**	**0.0018**
Type 4	**0.0032**	**0.0188**	-	**0.0039**	0.1243	**0.0001**
Type 1	**0.0001**	**0.002**	**0.0039**	**-**	**0.0135**	**0.0001**
ALY	**0.0001**	**0.0001**	0.1243	**0.0135**	**-**	**0.0001**
Type 5	**0.0001**	**0.0018**	**0.0001**	**0.0001**	**0.0001**	-

Table 6.6: p-values of pairwise comparisons of an NPMANOVA of the first four PC-scores of a between groups PCA on "A": a sample of all extant calcanei and the Trinil fossils (TRIN); and "B": a sample of all extant calcanei and Axis lydekkeri fossils (ALY), with significant values ($p<0.05$) in bold.

A visual assessment of the PCA scatterplot of the first two components in the Trinil analysis partially confirmed the results of the NPMANOVA. The same patterns that were described in the extant species model were still visible when PC1 was plotted against PC2 (Fig. 6.25). The Trinil specimens gave low scores on the first component. Although visual overlap between the different groups was substantial, Trinil clustered best with the type 1 and type 4 species. There was also some overlap with the type 3 and the type 2 groups, but these groups generally gave higher scores on PC1 and were also separated from the Trinil group on PC2. The type 5 specimens were well separated from the Trinil group and gave even higher scores than the type 3 group on PC1. The equivalent scatterplot of the PCA on the *Axis lydekkeri* analysis was almost identical to the one generated in the Trinil analysis (Fig. 6.25-A). Adding the extra *Axis lydekkeri* fossils did not interfere with specimen distribution along the axes. The *Axis lydekkeri* specimens gave low scores on PC1 and visually overlapped with the type 1 and type 4 groups. The type 2, type 3 and type 5 groups gave more positive scores on PC1.

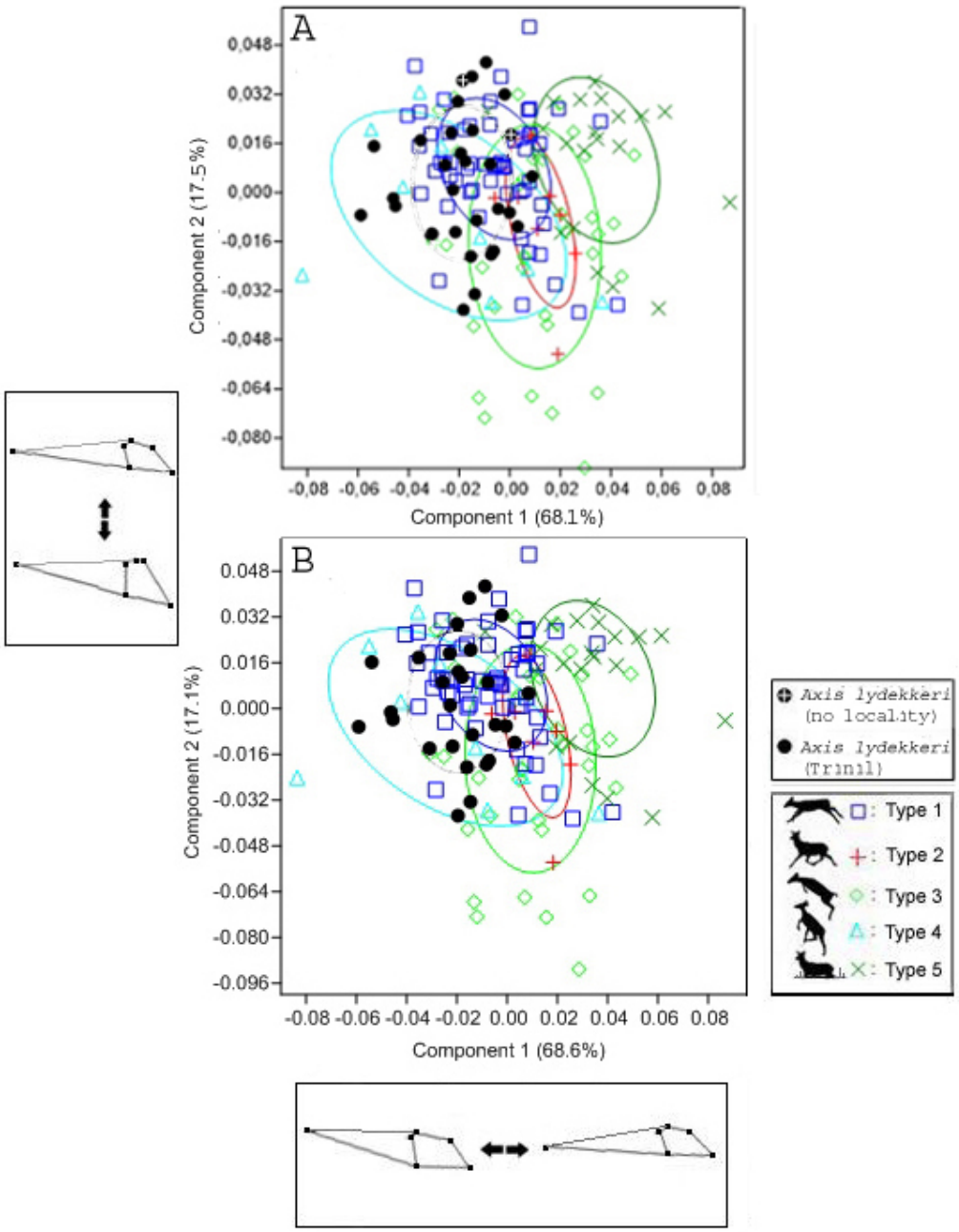


Figure 6.25: PC1 and PC2 scatterplot of a between groups PCA of: A: all extant calcanei and fossil Axis lydekkeri specimens, and B: all extant calcanei and fossil calcanei from Trinil. All extant specimens are ordered by habitat/locomotor strategy with 50% confidence intervals.

The Kruskal-Wallis test on the scores of PC1 of the Trinil analysis confirmed that overall between group differences were significant (H=65.49, p<0.0001). Pairwise comparisons gave significant differences between the Trinil group and the other groups on PC1 (Table 6.7-A).

Trinil differed significantly from the type 1 (p=0.008), type 2 (p<0.001), type 3 (p<0.001) and type 5 groups (p<0.001), but not from the type 4 group (p=0.5832), the latter group being similar to the type 1 group (p=0.0591). The Kruskal-Wallis test of the *Axislydekkeri* specimens indicated significant differences (H=66.7, p<0.0001). Pairwise comparisons (Table 6.7-B) showed that the *Axis lydekkeri* group differed significantly from the type 1 (p=0.0075), type 2 (p<0.001), type 3 (p<0.001) and type 5 groups (p<0.001), but not from the type 4 group (p=0.5819), the latter being more similar to the type 1 group (p=0.0699).

A: PC1 (TRIN)	Type 3	Type 2	Type 4	Type 1	TRIN	Type 5
Type 3	-	0.8637	**0.0081**	**0.0008**	**<0.0001**	**0.0001**
Type 2	0.8637	-	**0.0141**	**0.0044**	**<0.0001**	**0.0031**
Type 4	**0.0081**	**0.0141**	-	0.0591	0.5832	**0.0004**
Type 1	**0.0008**	**0.0044**	0.0591	-	**0.008**	**<0.0001**
TRIN	**<0.0001**	**<0.0001**	0.5832	**0.008**	**-**	**<0.0001**
Type 5	**0.0001**	**0.0031**	**0.0004**	**<0.0001**	**<0.0001**	-
A: PC2 (TRIN)	Type 3	Type 2	Type 4	Type 1	TRIN	Type 5
Type 3	-	0.5022	0.467	**0.0003**	**0.012**	**0.0013**
Type 2	0.5022	-	0.9616	**0.0091**	0.2616	**0.0428**
Type 4	0.467	0.9616	-	0.1255	0.313	0.1239
Type 1	**0.0003**	**0.0091**	0.1255	-	0.1486	0.2648
TRIN	**0.012**	0.2616	0.313	0.1486	-	0.1082
Type 5	**0.0013**	**0.0428**	0.1239	0.2648	0.1082	-

B: PC1 (ALY)	Type 3	Type 2	Type 4	Type 1	ALY	Type 5
Type 3	-	0.8392	**0.0081**	**0.0007**	**<0.0001**	**0.0002**
Type 2	0.8392	-	**0.0141**	**0.0041**	**<0.0001**	**0.0026**
Type 4	**0.0081**	**0.0141**	-	0.0699	0.5819	**0.0004**
Type 1	**0.0007**	**0.0041**	0.0699	-	**0.0075**	**<0.0001**
ALY	**<0.0001**	**<0.0001**	0.5819	**0.0075**	-	**<0.0001**
Type 5	**0.0002**	**0.0026**	**0.0004**	**<0.0001**	**<0.0001**	-
B: PC2 (ALY)	Type 3	Type 2	Type 4	Type 1	ALY	Type 5
Type 3	-	0.5022	0.5412	**0.0003**	**0.0075**	**0.0011**
Type 2	0.5022	-	0.9616	**0.0102**	0.244	**0.0381**
Type 4	0.5412	0.9616	-	0.1302	0.2436	0.094
Type 1	**0.0003**	**0.0102**	0.1302	-	0.228	0.2195
ALY	**0.0075**	0.244	0.2436	0.228	-	0.1407
Type 5	**0.0011**	**0.0381**	0.094	0.2195	0.1407	-

Table 6.7: Mann-Whitney pairwise comparisons of a Kruskal-Wallis test for PC1 and PC2 of the bg- PCA on all extant calcanei and A: Trinil fossils (TRIN); B: A. lydekkeri fossils (ALY), significant values (p<0.05) in bold.

In sum, specimen distribution along the first axis indicated that the fossils from Trinil and the unprovenanced *Axis lydekkeri* calcanei had a shape similar to that of cervids associated with a cursorial behaviour or somewhat saltatorial behaviour but with a capacity for high endurance and speed, attributes found in animals of more open or mountainous environments. This was morphologically expressed in relatively short calcanei with a tuber that was positioned at a higher angle relative to the anterior portion of the calcaneus (see Fig. 6.1). Because the shape variation explained by PC1 was probably to a substantial extent functionally correlated (see section 6.2.1), it was likely that the patterns described by the Trinil group were ecomorphologically significant.

As in the extant species model, PC2 (Fig. 6.25) gave substantially more visual overlap than PC1. The Trinil specimens gave high scores on this axis together with the type 1, type 4 and the type 5 specimens (Fig. 6.25-B). The type 2 and type 3 groups gave somewhat lower scores. In the scatterplot with PC1, Trinil mainly clustered with the type 1 and type 4 specimens and was visually relatively well separated from the type 2 and 3 specimens. The position of the *Axis lydekkeri* group along the second axis (Fig. 6.26-A) was very similar to that of the Trinil group. The fossil *Axis lydekkeri* specimens gave high scores on PC2, together with the type1, type 4 and type 5 specimens, while the type 2 and type 3 groups gave low scores. Plotted against PC1 (Fig. 6.25-A), the fossils clustered with the type 1 and type 4 groups.

The Kruskal-Wallis test on the Trinil specimens indicated significant differences between groups on the second axis (H=21.8, p=0.0005). The between group differences visually observed in the scatterplots were in part confirmed by the pairwise comparisons (Table 6.7). The Trinil group was significantly different from the type 3 group on this axis (p=0.012). No significant differences were found between the Trinil group and the type 1 (p=0.1486), type 2 (p=0.2616), type 4 (p=0.3130) and type 5 specimens (p=0.1082), implying that the shape of

the Trinil calcanei, as summarized by this axis, was perhaps most similar to that of type 1, type 2 and type 4 species. The same trends were mirrored in the *Axis lydekkeri* analysis. In addition to the significant group differences measured in the Kruskal-Wallis test (H=21.8, p=0.0005), the *Axis lydekkeri* group was in the pairwise comparisons shown to be significantly different from the type 3 group on the second axis. *P*-values were even lower than in the Trinil analysis (p=0.0075). No significant differences were found between the *Axis lydekkeri* group and the type 1 (p=0.228), type 2 (p=0.244), type 4 (p=0.2436) and type 5 specimens (p=0.1407).

In terms of morphology, this meant that the calcanei from Trinil and the unprovenanced *Axis lydekkeri* specimens had relatively long articular surfaces supporting the malleolus, a trait not usually associated with more saltatorial species, adapted to closed environments and wet substrate (see Fig. 6.4). This morphotype is more likely to be found in species of dry, open or intermediate environments (possibly at high altitude) that require a more cursorial behaviour. However, on this axis the type 5 specimens, associated with cursorial behaviour and open, wet environments, also gave high scores like the type 1 and type 4 groups. Consequently, the specimens from Trinil and the other *Axis lydekkeri* specimens were also morphologically similar to a morphotype associated with open, wet environments. In the extant species model (section 6.2.1) the morphological variation explained by the second component was considered at least in part functionally correlated. It could therefore be concluded that the patterns described by the Trinil and *Axis lydekkeri* groups along this axis were ecomorphologically significant.

On PC3 and PC4 visual separation between the different groups was minimal. On the third component only the type 3 group was somewhat separated from the main cluster of specimens in the Trinil and *Axis lydekkeri* analyses, but the Kruskal-Wallis test provided only limited support for these separations (Appendix L). Similarly, on PC4, there was too much visual

overlap to discern any meaningful patterns (Appendix L). Furthermore, the few visual separations that were observed along PC3 and PC4, were not considered particularly relevant to this ecomorphological study. As mentioned in section 6.2.1.3, the lack of meaningful patterns and the absence of a clear functional correlation for these axes in the extant model, made it doubtful that the morphological variation explained by PC3 and PC4, and therefore the position of the fossil groups, was ecomorphologically significant.

In summary it could be concluded from the results of the Trinil and *Axis lydekkeri* analyses that the fossil *Axis lydekkeri* calcanei (from Trinil) were most similar in shape to those of cursorial animals of open, dry environment, potentially of high altitude. The morphotype associated with such a high elevation environment was, nevertheless, very similar to that of lowland species adapted to dry, open environments and possibly indistinguishable. When taking only those shape components into account that were considered ecomorphologically significant (PC1 and PC2), the same pattern surfaced: the Trinil fossils and the unprovenanced *Axis lydekkeri* fossils conformed to a morphotype typical of cursorial species adapted to dry, open environment, possibly of high altitude (PC1), but certainly not like that of saltatorial species, adapted to wet, closed environment (PC2).

6.3.1.3 Intermediate phalanx

The results of the NPMANOVA on PC1 to PC4 resulted in significant between group differences (F=15.43, p=0.0001). Pairwise comparisons (Table 6.8) in part revealed the same differences between individual groups that were observed in the extant species analysis (see section 6.2.2.4). As in the model, significant differences were lacking between the type 2 group and the type 4 (p=0.3058) and type 5 groups (p=0.1068) in the Trinil analysis (Table 6.8-A). Adding the Trinil fossils to the extant dataset altered specimen between-group relationships to a certain extent in the type 5 group, as additional non-significant differences

were measured between this group and the type 3 (p=0.2421) and type 4 group (p=0.1941). As far as the fossils were concerned, it was indicated that the Trinil specimens were significantly different from the type 1 (p=0.0001), type 2 (p=0.0006), type 3 (p=0.0001), type 4 (p=0.0033), type 5 (p=0.0034) and type 6 groups (p=0.0001). The results suggested that the intermediate phalanges from Trinil were different in multidimensional space from all extant groups.

A (TRIN)	Trinil	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Trinil	-	**0.0001**	**0.0006**	**0.0001**	**0.0033**	**0.0034**	**0.0001**
Type 1	**0.0001**	-	**0.0073**	**0.0001**	**0.0128**	**0.0001**	**0.0001**
Type 2	**0.0006**	**0.0073**	-	**0.0008**	0.3058	0.1068	**0.0003**
Type 3	**0.0001**	**0.0001**	**0.0008**	-	**0.0195**	0.2421	**0.0001**
Type 4	**0.0033**	**0.0128**	0.3058	**0.0195**	-	0.1941	**0.004**
Type 5	**0.0034**	**0.0001**	0.1068	0.2421	0.1941	-	**0.0005**
Type 6	**0.0001**	**0.0001**	**0.0003**	**0.0001**	**0.004**	**0.0005**	-

B (ALY)	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	ALY
Type 1	-	**0.0073**	**0.0001**	**0.0288**	**0.0001**	**0.0001**	**0.0001**
Type 2	**0.0073**	-	**0.0015**	0.4792	0.0971	**0.0002**	**0.0014**
Type 3	**0.0001**	**0.0015**	-	**0.0027**	**0.012**	**0.0001**	**0.0008**
Type 4	**0.0288**	0.4792	**0.0027**	-	**0.0383**	**0.0051**	**0.0029**
Type 5	**0.0001**	0.0971	**0.012**	**0.0383**	-	**0.001**	**0.0055**
Type 6	**0.0001**	**0.0002**	**0.0001**	**0.0051**	**0.001**	-	**0.0001**
ALY	**0.0001**	**0.0014**	**0.0008**	**0.0029**	**0.0055**	**0.0001**	-

Table 6.8: p-values of pairwise comparisons of an NPMANOVA of the first four PC-scores of a between groups PCA on all extant intermediate phalanges and A: all Trinil fossils (TRIN); B: all Axis lydekkeri fossils (ALY), with significant values ($p<0.05$) in bold.

Adding the unprovenanced *Axis lydekkeri* specimens to the dataset did not result in substantial differences compared to the Trinil analysis, although some discrepancies were noted (Table 6.8-B). In the more extended *Axis lydekkeri* analysis the NPMANOVA also suggested significant between group differences (F=14.02, p=0.0001), but pairwise comparisons of the extant habitat groups suggested a closer similarity to the patterns observed in the extant species model (see Table 6.5). In the *Axis lydekkeri* analysis, non-significant differences were

only measured between the type 2 and the type 4 group (p=0.4792) and between the type 2 and the type 5 group (p=0.0971). The *Axis lydekkeri* specimens were significantly different from the type 1 (p=0.0001), type 2 (p=0.0014), type 3 (p=0.0008), type 4 (p=0.0029), type 5 (p=0.0055) and type 6 groups (p=0.0001). The phalanges were significantly different in multidimensional space from all extant groups, but with perhaps the highest similarity to the type 4 and the type 5 groups.

The results of the NPMANOVA and the associated pairwise comparisons were in line with those of the PCA scatterplots of PC1 and PC2 (Fig. 6.26). In the Trinil analysis the same patterns were visible for the habitat/locomotor groups as in the extant model. Despite overlap between most of the groups, the Trinil specimens generally gave high scores on this axis, together with the type 3, type 5 and type 6 groups. The type 2 specimens were intermediate and the type 4 and type 1 specimens gave lower scores. When PC1 was plotted against PC2 (Fig. 6.26-A), the fossils visually clustered best with the type 5 group. In the *Axis lydekkeri* analysis, the same patterns were visible as in the extant model and the Trinil analysis. On PC1 (Fig. 6.26-B), the *Axis lydekkeri* specimens gave low scores with the type 3, type 5 and type 6 specimens. The type 1 and type 4 specimens gave higher scores, while the type 2 specimens were intermediate. When PC1 was plotted against PC2 (Fig. 6.26-B), the *Axis lydekkeri* fossils clustered best with the type 3 and type 5 groups.

The Kruskal-Wallis test on the Trinil specimens indicated significant differences between groups along the first axis (H=22.07, p=0.0011). Pairwise comparisons for the largest part gave the same significant differences between the habitat/locomotor groups as in the extant species model (Table 6.9-A). The only exception was the type 6 group. Where this group was still significantly different from all other groups on PC1 in the extant model (see Table 6.5), in the Trinil analysis the data was somewhat altered by the addition of the extra specimens. Consequently, significant differences were only measured between the type 6 group and the

type 1 (p<0.0001) and type 2 groups (p=0.0108). The group of Trinil fossils was significantly different from the type 1 (p<0.0001), type 2 (p=0.0081) and type 4 groups (p=0.0491). No significant differences were measured between the Trinil group and the type 3 (p=0.189), type 5 (p=0.2937) and type 6 specimens (p=0.7898), suggesting a similarity between the Trinil deer and the latter groups.

The Kruskal-Wallis test on the *Axis lydekkeri* dataset also indicated significant differences between groups along the first axis (H=61.89, p<0.0001). This was largely confirmed by the pairwise comparisons (Table 6.9-B). Significant separations along PC1 were mostly the same as in the Trinil analysis, although some discrepancies were noted. The type 2 group was significantly different from the type 1 group (p=0.033). The type 3 group was significantly different from the type 4 group (p=0.0432), but not from the type 6 group (p=0.9831). Furthermore, the type 6 group was in the *Axis lydekkeri* analysis not significantly different from the type 4 (p=0.0673) and type 5 groups (p=0.6718). As far as the fossil specimens were concerned, the *Axis lydekkeri* group was significantly different from the type 1 (p<0.0001), type 2 (p=0.0069) and type 4 groups (p=0.0295) on the first axis. The fossils were not significantly different from the type 3 (p=0.3853), type 5 (p=0.3682) and type 6 groups (p=0.3756). The results in other words largely mirrored those of the Trinil analysis. The extra *Axis lydekkeri* specimens in the dataset did not alter the originally observed patterns on PC1 in the more limited analysis of the Trinil fossils.

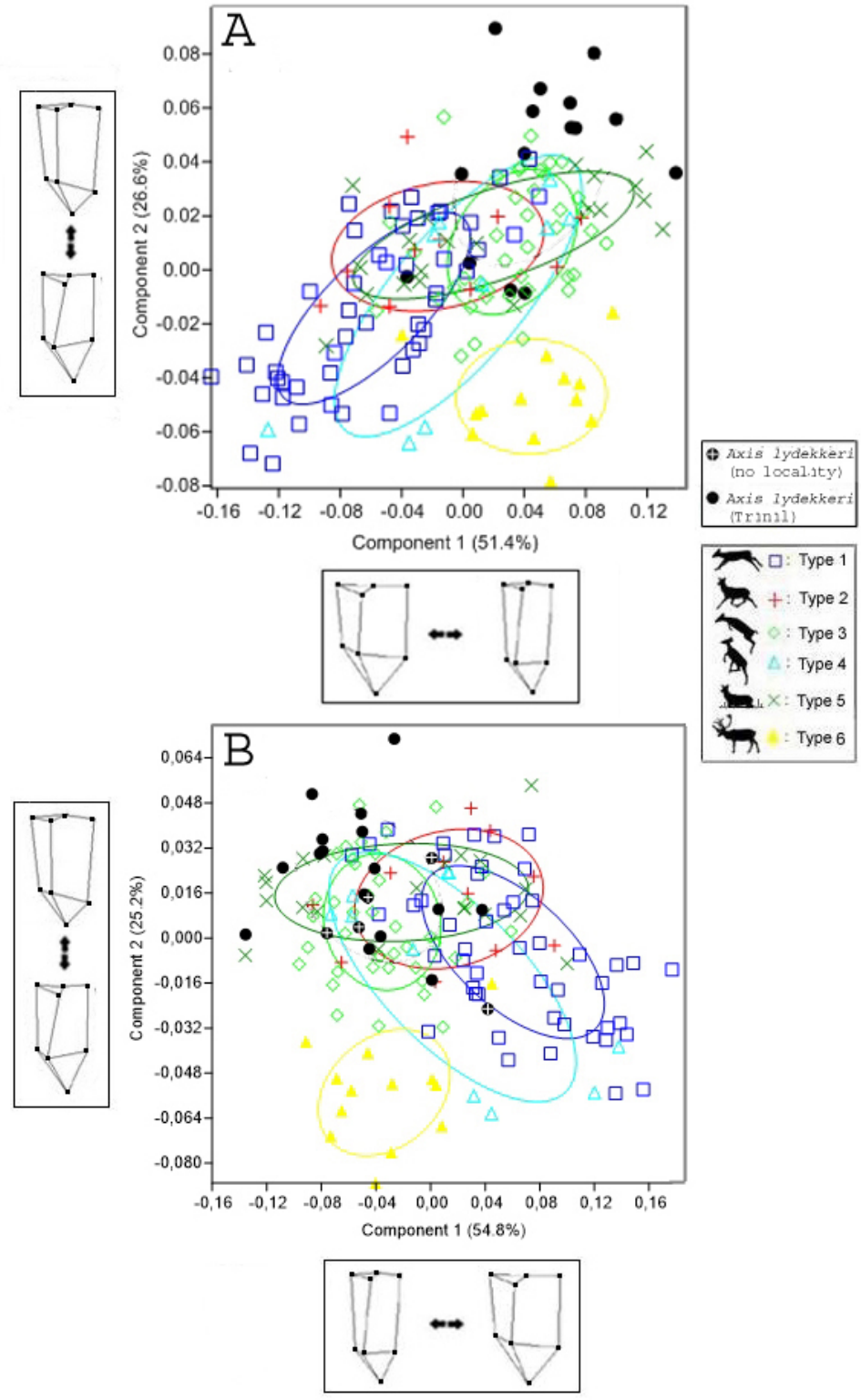


Figure 6.26: PC1 and PC2 scatterplot of a between groups PCA of: A: all extant phalanges and fossil phalanges from Trinil, and B: all extant calcanei and fossil Axis lydekkeri specimens. All extant specimens are ordered by habitat/locomotor strategy with 50% confidence intervals.

A: PC1 (TRIN)	TRIN	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
TRIN	-	**<0.0001**	**0.0081**	0.189	**0.0491**	0.2937	0.7898
Type 1	**<0.0001**	-	0.0528	**<0.0001**	**0.0101**	**0.0002**	**<0.0001**
Type 2	**0.0081**	0.0528	-	**0.0076**	0.4941	0.1543	**0.0108**
Type 3	0.189	**<0.0001**	**0.0076**	-	0.0958	0.5051	0.211
Type 4	**0.0491**	**0.0101**	0.4941	0.0958	-	0.5877	0.0713
Type 5	0.2937	**0.0002**	0.1543	0.5051	0.5877	-	0.4501
Type 6	0.7898	**<0.0001**	**0.0108**	0.211	0.0713	0.4501	-
A: PC2 (TRIN)	TRIN	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
TRIN	-	**<0.0001**	**0.0147**	**0.0014**	**0.0072**	**0.0059**	**<0.0001**
Type 1	**<0.0001**	-	**0.0271**	**0.0002**	0.751	**0.0007**	**0.0003**
Type 2	**0.0147**	**0.0271**	-	0.8457	0.5433	0.47	**<0.0001**
Type 3	**0.0014**	**0.0002**	0.8457	-	0.2839	0.5994	**<0.0001**
Type 4	**0.0072**	0.751	0.5433	0.2839	-	0.2116	0.0825
Type 5	**0.0059**	**0.0007**	0.47	0.5994	0.2116	-	**<0.0001**
Type 6	**<0.0001**	**0.0003**	**<0.0001**	**<0.0001**	0.0825	**<0.0001**	-

B: PC1 (ALY)	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	ALY
Type 1	-	**0.033**	**<0.0001**	**0.0447**	**0.0002**	**<0.0001**	**<0.0001**
Type 2	**0.033**	-	**0.0065**	0.9719	0.2079	**0.037**	**0.0069**
Type 3	**<0.0001**	**0.0065**	-	**0.0432**	0.4962	0.9831	0.3854
Type 4	**0.0447**	0.9719	**0.0432**	-	0.2811	0.0673	**0.0295**
Type 5	**0.0002**	0.2079	0.4962	0.2811	-	0.6718	0.3682
Type 6	**<0.0001**	**0.037**	0.9831	0.0673	0.6718	-	0.3756
ALY	**<0.0001**	**0.0069**	0.3854	**0.0295**	0.3682	0.3756	-
B: PC2 (ALY)	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	ALY
Type 1	-	**0.03**	**0.0481**	0.5035	**0.0032**	**<0.0001**	**0.0012**
Type 2	**0.03**	-	0.2813	0.1131	0.8526	**<0.0001**	0.5518
Type 3	**0.0481**	0.2813	-	0.2014	**0.0479**	**<0.0001**	**0.0324**
Type 4	0.5035	0.1131	0.2014	-	**0.0263**	**0.02**	**0.0169**
Type 5	**0.0032**	0.8526	**0.0479**	**0.0263**	-	**<0.0001**	0.686
Type 6	**<0.0001**	**<0.0001**	**<0.0001**	**0.02**	**<0.0001**	-	**<0.0001**
ALY	**0.0012**	0.5518	**0.0324**	**0.0169**	0.686	**<0.0001**	-

Table 6.9: p-values of Mann-Whitney pairwise comparisons of a Kruskal-Wallis test for PC1 and PC2 of the bg-PCA on all extant phalanges and: A: Trinil fossils (TRIN); B: Axis lydekkeri fossils (ALY), with significant values ($p<0.05$) in bold.

Based on the visual assessment of the scatterplots associated with PC1 and the Kruskal-Wallis tests, it could be concluded that the intermediate phalanges from Trinil and the unprovenanced *Axis lydekkeri* phalanges were most similar in shape to those of cervids found

in open or closed environments with wet, yielding substrate, or more unlikely, to those of tundra species. Morphologically this meant that the *Axis lydekkeri* phalanges and the fossils from Trinil were relatively gracile, a trait associated with an increased capacity for splaying in taxa adapted to wet, yielding substrates (see section 6.2.2.4). As the variation in this trait was linked to the functional hypotheses proposed for the phalanx, it was likely that the patterns described by the fossils on this axis were ecomorphologically significant.

On PC2 in the Trinil analysis, the type 1 specimens gave relatively low scores, while the type 3 and type 5 specimens gave high scores. Type 2 specimens were intermediate and type 4 specimens were more dispersed over the scatterplot (Fig. 6.25-A). Where in the extant species model the type 6 group gave intermediate scores, in the Trinil analysis the type 6 specimens gave scores more similar to the type 1 group. Apparently the placement of this group on the second axis was somewhat altered by the addition of the fossil specimens, but the observation that the type 6 group gave different results on PC2 than on PC1 was still confirmed. The Trinil specimens themselves gave high scores on the second axis, similar to the type 3 and type 5 groups, sometimes even exceeding the highest scores of the latter groups. In the scatterplot with PC1 (Fig. 6.25-A), the Trinil group also clustered best with these two extant groups. Adding the unprovenanced *Axis lydekkeri* specimens to the dataset resulted in broadly similar patterns (Fig. 6.25-B). Notwithstanding, the position of the type 6 group was somewhat altered, relative to the extant species model. The *Axis lydekkeri* group itself gave positive scores on PC2, like the type 3, type 5 and type 6 groups. Where in the Trinil analysis the fossil specimens gave scores that sometimes exceeded that of the type 3 and type 5 groups, in the *Axis lydekkeri* analysis the fossil specimens appeared to be more within the normal range of these two extant groups. When PC2 was plotted against PC1 (Fig. 6.25-B), the fossil group clustered best with the type 3 and type 5 groups.

The Kruskal-Wallis test on the Trinil specimens indicated significant between group differences along the second axis (H=57.99, p<0.0001). Pairwise comparisons (Table 6.9-A) confirmed part of the differences observed on the second axis in the extant species model. Differences were mostly the same, except that the type 3 group was not significantly different from the type 2 (p=0.8457) and type 4 groups (p=0.2839) anymore. Moreover, the better separation of the type 6 group in the scatterplots (Fig. 6.29) also led to additional significant differences. Significant differences were measured between the type 6 group and the type 2 (p<0.0001), type 5 (p<0.0001), type 1 (p=0.0003) and type 3 groups (p<0.0001). The fossil Trinil specimens were significantly different from the type 1 (p<0.0001), type 2 (p=0.0147), type 3 (p=0.0014), type 4 (p=0.0072), type 5 (p=0.0059) and type 6 groups (p<0.0001).

The Kruskal-Wallis test (H=49.08, p<0.0001) and associated pairwise comparisons (Table 6.9-B) on the more extended *Axis lydekkeri* dataset, generally confirmed these patterns for the second axis, but some differences were noted. Especially the type 5 group was better separated than in the extant model and the Trinil analysis. In the *Axis lydekkeri* analysis this group was also significantly different from the type 3 (p=0.0479) and type 4 groups (p=0.0263). Additional significant differences were also measured between the type 6 group and the type 3 group (p<0.0001) and type 6 group and type 4 group (p=0.02). Contrary to the extant model, the type 3 group was not significantly different from the type 2 (p=0.2813) and type 4 groups (p=0.2014), like in the Trinil analysis.

As far as the *Axis lydekkeri* specimens themselves were concerned, separations were not as well supported by the pairwise comparisons as in the Trinil analysis. Significant differences were measured between the Trinil group and all extant habitat/locomotor groups, but the larger *Axis lydekkeri* sample was not significantly different from the type 2 (p=0.5518) and type 5 groups (p=0.686). Significant differences were, on the other hand, measured between

the *Axis lydekkeri* fossils and the type 1 (p=0.0012), type 3 (p=0.0324), type 4 (p=0.0169) and type 6 specimens (p<0.0001).

In sum, the visual assessments of specimen distributions along the second component and the results of the Kruskal-wallis test and the associated pairwise comparisons, indicated that the phalanges from Trinil and the unprovenanced *Axis kydekkeri* specimens were morphologically different from those of cursorial deer adapted to open environments with a dry substrate. The morphology of the Trinil phalanges was more similar to that of saltatorial forms of closed environments with wet substrates, or perhaps more likely, to that of somewhat cursorial forms found in open environments with wet, yielding substrates.

In morphological terms this meant that the phalanges had relatively shallow proximal articular surfaces, a trait more typical of species adapted to environments with wet, yielding substrates. The results also implied that in the *Axis lydekkeri* fossils (from Trinil) the placement of the extensor process on the anterior side of the phalanx was relatively low. This is a trait more typical of forms found in closed or open environments with wet, yielding substrates. As the morphological variation summarized by the second component was linked to the functional hypotheses proposed for the intermediate phalanx, it was likely that the patterns described by the Trinil fossils along this axis were ecomorphologically significant.

PC3 and PC4 were retained as relevant components (for the NPMANOVA) as they explained a substantial amount (see Appendix M) of real shape variance in the PCA. On PC3 in the Trinil and *Axis lydekkeri* analyses, separations were somewhat better than in the extant species model. In these analyses the type 1 group, together with the fossil specimens, gave somewhat higher scores on this axis than the rest of the specimens. These separations were confirmed by the Kruskal-Wallis test and the pairwise comparisons (see Appendix M). On PC4 all groups tended to cluster in the center of the graph and visual overlap obscured all

possible patterns. The extant species analysis, however, indicated that the morphological changes along PC3 and PC4 were not to a large extent functionally driven. The ecomorphological significance of these shape components was therefore probably limited.

In summary it could be concluded from the results of the Trinil analysis and of the unprovenanced *Axis lydekkeri* calcanei, that the fossils were, generally speaking, most similar in morphology to those of somewhat cursorial species, adapted to open environments with wet substrate. A more specific assessment of the shape components that were considered ecomorphologically most significant (PC1 and PC2) confirmed a similarity to wet, open environment cervids, or alternatively to cervids adapted to a more closed environment with wet substrate.

6.3.2 Kedung Brubus and *Cervus kendengensis*

6.3.2.1 Introduction

For this analysis a small dataset of six *Cervus kendengensis* calcanei, associated with the Kedung Brubus faunal unit, was appended to the extant species model. This resulted in a combined dataset of 131 specimens (see Tables 5.2 and 5.3). In addition, a sample of five *Cervus kendengensis* phalanges from the Kedung Brubus faunal unit was combined with the extant model, resulting in a dataset of 147 specimens (see Tables 5.2 and 5.3). Each combination was resubmitted to a new GPA, followed by a bg-PCA on the procrustes residuals. Due to small sample size, only one analysis was run for each element. No separate analyses were conducted on material from the different localities that form part of the Kedung Brubus faunal unit. A table with eigenvalues and broken stick distributions associated with the PCA were provided in Appendices J (calcaneus) and K (intermediate phalanx).

6.3.2.2 Calcaneus

An NPMANOVA on the scores of PC1 to PC4 indicated significant between group differences (F=7.55, p=0.0001). Pairwise comparisons (Table 6.10) gave the same significant differences also observed between the habitat/locomotion groups in the extant species model (see section 6.2.1.3). For the habitat/locomotion groups, differences were only non-significant between the type 2 and the type 3 specimens (p=0.4706). Adding the *Cervus kendengensis* fossils did not interfere with the patterns described by the extant species model. The *Cervus kendengensis* sample was found to be significantly different from the type 3 (p=0.0259), type 4 (p=0.0202) and type 5 groups (p<0.001) in multidimensional space.

The NPMANOVA and associated pairwise comparisons indicated that the *Cervus kendengensis* calcanei, associated with the Kedung Brubus faunal unit, were morphologically most similar to the cursorial extant forms, more likely to be found in dry, open or intermediate environments. The morphology of the fossil calcanei was different from that of more saltatorial species of closed environments or wet, open environment forms.

	Type 3	CKE	Type 2	Type 4	Type 1	Type 5
Type 3	-	**0.0259**	0.4706	**0.0044**	**0.0001**	**0.0001**
CKE	**0.0259**	-	0.0624	**0.0202**	0.055	**0.0006**
Type 2	0.4706	0.0624	-	**0.0164**	**0.0008**	**0.0067**
Type 4	**0.0044**	**0.0202**	**0.0164**	-	**0.0026**	**0.0001**
Type 1	**0.0001**	0.055	**0.0008**	**0.0026**	-	**0.0001**
Type 5	**0.0001**	**0.0006**	**0.0067**	**0.0001**	**0.0001**	-

Table 6.10: p-values of pairwise comparisons of an NPMANOVA of the first four PC-scores of a between groups PCA on all extant calcaneus specimens and the Cervus kendengensis fossils (CKE) from a number of Kedung Brubus sites, with significant values (p<0.05) in bold.

A visual assessment of the PCA scatterplot of PC1 and PC2 (Fig. 6.27) revealed patterns that were in line with the results produced by the NPMANOVA. Generally speaking, specimens

behaved in a similar way as in the extant species model. As a group, the *Cervus kendengensis* specimens gave relatively low scores on the first axis, together with the type 1 and type 4 groups. The type 3 and type 5 groups gave more positive scores. The type 2 group was intermediate. Overall, the *Cervus kendengensis* group clustered best with the type 1 group in the scatterplot. Pairwise comparisons following a Kruskal-Wallis test (H=49.24, p<0.0001) on the scores of PC1 only partially confirmed the visual separations (Table 6.11). For most extant habitat/locomotor groups, significant differences were measured on the first axis. Notable exceptions were differences between the type 2 and type 3 group (p=0.8149) and between the type 1 and type 4 group (p=0.07902). The *Cervus kendengensis* specimens were, however, only significantly different from the type 5 group (p=0.00148). *P*-values were especially high between the fossil group and the type 1 group (p=0.6147).

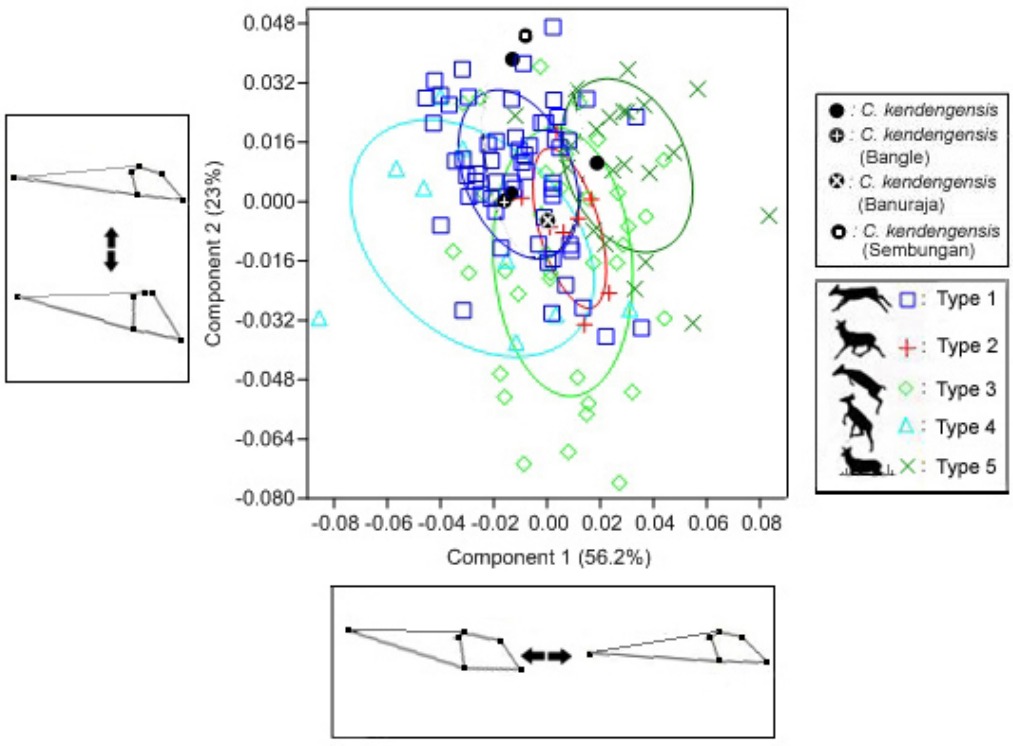


Figure 6.27: PC1 and PC2 scatterplot of a between groups PCA of all extant calcanei and fossil Cervus kendengensis calcanei ordered by habitat/locomotor strategy with 50% confidence intervals.

PC1	Type 3	CKE	Type 2	Type 4	Type 1	Type 5
Type 3	-	0.2166	0.8149	**0.0068**	**0.0006**	**0.0003**
CKE	0.2166	-	0.0612	0.1753	0.6147	**0.0014**
Type 2	0.8149	0.0612	-	**0.0141**	**0.0036**	**0.0031**
Type 4	**0.0068**	0.1753	**0.0141**	-	0.079	**0.0003**
Type 1	**0.0006**	0.6147	**0.0036**	0.079	-	**<0.0001**
Type 5	**0.0003**	**0.0014**	**0.0031**	**0.0003**	**<0.0001**	-
PC2	Type 3	CKE	Type 2	Type 4	Type 1	Type 5
Type 3	-	**0.0233**	0.5637	0.6209	**0.0001**	**0.0013**
CKE	**0.0233**	-	0.0612	0.1407	0.7167	0.7484
Type 2	0.5637	0.0612	-	0.8852	**0.0259**	**0.0299**
Type 4	0.6209	0.1407	0.8852	-	**0.0476**	**0.0417**
Type 1	**0.0001**	0.7167	**0.0259**	**0.0476**	-	0.492
Type 5	**0.0013**	0.7484	**0.0299**	**0.0417**	0.492	-

Table 6.11: p-values of Mann-Whitney pairwise comparisons of a Kruskal-Wallis test for PC1 and PC2 of the bg- PCA on all extant calcaneus specimens and Cervus kendengensis fossils (CKE), with significant values ($p<0.05$) in bold.

All things considered, the position of the *Cervus kendengensis* group along PC1 suggested that the calcaneus of this form, associated with the Kedung Brubus faunal unit, had a relatively short tuber calcanei that was positioned at a higher angle relative to the anterior portion of the bone, a trait usually found in cursorial species of dry, open environment. Although statistical strength was limited, it was likely that *Cervus kendengensis* was closest in morphology to the type 1 species. It was morphologically different from that of species found in wet, open environments. As the morphological variation explained by PC1 was most likely functionally driven to a substantial extent (see section 6.2.1), the above described patterns should be considered ecomorphologically significant.

The patterns visually observed in the extant species model were also not altered on the second axis in the *Cervus kendengensis* analysis (Fig. 6.27). The *Cervus kendengensis* specimens gave high scores on PC2, together with the type 1, type 4 and type 5 specimens. The type 2 and type 3 groups gave lower scores. When PC2 was plotted against PC1 (Fig. 6.27), the

fossils clustered fairly well with the type 1 group. In pairwise comparisons (Table 6.11) following a Kruskal-Wallis test (H=23.6, p=0.0002) the same between-group differences were found as in the extant species model. The type 4 group even gave somewhat better separations on the second axis than in the model. In the *Cervus kendengensis* analysis, the type 1 group was significantly different from the type 2 (p=0.02598), type 4 (p=0.04763) and type 3 groups (p<0.001). The type 5 group was significantly different from the type 2 (p=0.0299), type 3 (p=0.001302) and type 4 groups (p=0.0417). No significant differences were, however, found between the fossil *Cervus kendengensis* specimens and most of the other groups on this axis, with the exception of the type 3 group (p=0.0233).

Taking into account the results of the Kruskal-Wallis test, the associated multiple comparisons and the visual assessment of specimen distribution along the second axis, it could be concluded that the calcaneus of the *Cervus kendengensis* specimens from the Kedung Brubus faunal unit had comparatively long articular surfaces supporting the malleolus. Although stastical strength was limited for the fossil group, this trait is usually found in more cursorial, or at least intermediate species, associated with either dry or wet open environments or mountainous environments. It was, nevertheless, relatively certain that the *Cervus kendengensis* calcanei were unlike those found in saltatorial animals associated with closed environments with wet substrates.

On the third and fourth axis, visual overlap between the different groups was substantial. On the third axis, only the type 2 specimens, together with the fossils gave somewhat lower scores. On PC4 no clear patterns were visually discerned and all groups tended to cluster in the center of the scatterplot (see Appendix L). Despite that PC3 and PC4 were retained as relevant components in the extant species analysis, and explained real shape variation between the different calcaneus specimens, the extant species analysis suggested that most of the morphological variation summarized by these axes was not to a large extent functionally

driven. The third and fourth components were therefore considered of limited ecomorphological significance. The scatterplots, the results of the Kruskal-Wallis test and of the pairwise comparisons can be found in Appendix L.

In summary it could be concluded from the results of the *Cervus kendengensis* analysis that the calcanei from the Kedung Brubus faunal unit were similar in shape to those of cursorial cervids, adapted to dry, open environments, possibly of high elevation. The *Cervus kendengensis* calcanei were different in shape from calcanei of species with a saltatorial locomotor strategy, adapted to closed, wet environments or from those linked with open, wet environments. The more specific assessment of the ecomorphologically significant components (mainly PC1 and PC2) confirmed this and further specified that the fossils were probably more allied to open, dry environment forms, associated with lowland.

6.3.2.3 Intermediate phalanx

The results of the NPMANOVA on the first four components (F=7.48, p<0.0001) confirmed the between group-differences that were observed in the extant species model (section 6.2.2.4). The associated pairwise comparisons (Table 6.12) indicated that the fossil specimens were significantly different from the type 1 (p=0.0001), type 2 (p=0.0009), type 3 (p=0.0001), type 4 (p=0.0069), type 5 (p=0.003) and type 6 groups (p=0.0002). Alternatively, the results suggested that the *Cervus kendengensis* phalanges from the Kedung Brubus faunal unit were significantly different in multidimensional space from all extant groups, but with possibly the highest similarity to the type 4 and type 5 groups.

A visual assessment of the scatterplot associated with the first two components, gave some further insight into the relationships between the habitat/locomotor groups and the fossil group (Fig. 6.28). The results of the NPMANOVA and pairwise comparisons were partially confirmed by specimen positions in the scatterplots. On the first axis the patterns described by

the habitat/locomotor groups were almost identical to those described in the extant species model. This was not surprising as the small sample size of the *Cervus kendengensis* group was probably not able to alter specimen relationships to a large extent in the dataset. Although there was substantial overlap between most of the groups, the *Cervus kendengensis* specimens gave intermediate to high scores on the first axis, similar to the type 1, type 2 and part of the type 4 group. When PC1 was plotted against PC2 (Fig. 6.28), the fossils visually clustered best with the type 1, type 4 and type 5 groups.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	CKE
Type 1	-	**0.0094**	**0.0001**	**0.0267**	**0.0001**	**0.0001**	**0.0001**
Type 2	**0.0094**	-	**0.0021**	0.4193	0.1124	**0.0001**	**0.0009**
Type 3	**0.0001**	**0.0021**	-	**0.0023**	**0.009**	**0.0001**	**0.0001**
Type 4	**0.0267**	0.4193	**0.0023**	-	**0.0367**	**0.0044**	**0.0069**
Type 5	**0.0001**	0.1124	**0.009**	**0.0367**	-	**0.0006**	**0.003**
Type 6	**0.0001**	**0.0001**	**0.0001**	**0.0044**	**0.0006**	-	**0.0002**
CKE	**0.0001**	**0.0009**	**0.0001**	**0.0069**	**0.003**	**0.0002**	-

Table 6.12: p-values of pairwise comparisons of an NPMANOVA of the first four PC-scores of a between groups PCA on all extant intermediate phalanges and the Cervus kendengensis fossils (CKE), with significant values ($p<0.05$) in bold.

The Kruskal-Wallis test resulted in significant differences between group medians (H=62.09, p<0.0001). Pairwise comparisons (Table 6.13) showed that the same significant differences were observed between the habitat/locomotor groups as in the extant species model (Table 6.5). This meant that the fossils specimens did not alter the between-group relationships observed in the model. The *Cervus kendengensis* fossils were significantly different from the type 3 (p=0.006209) and the type 6 groups (p=0.005779) on this axis, but not significantly different from the type 1 (p=0.1662), type 2 (p=0.4278), type 4 (p=0.5815) and type 5 groups (p=0.9729).

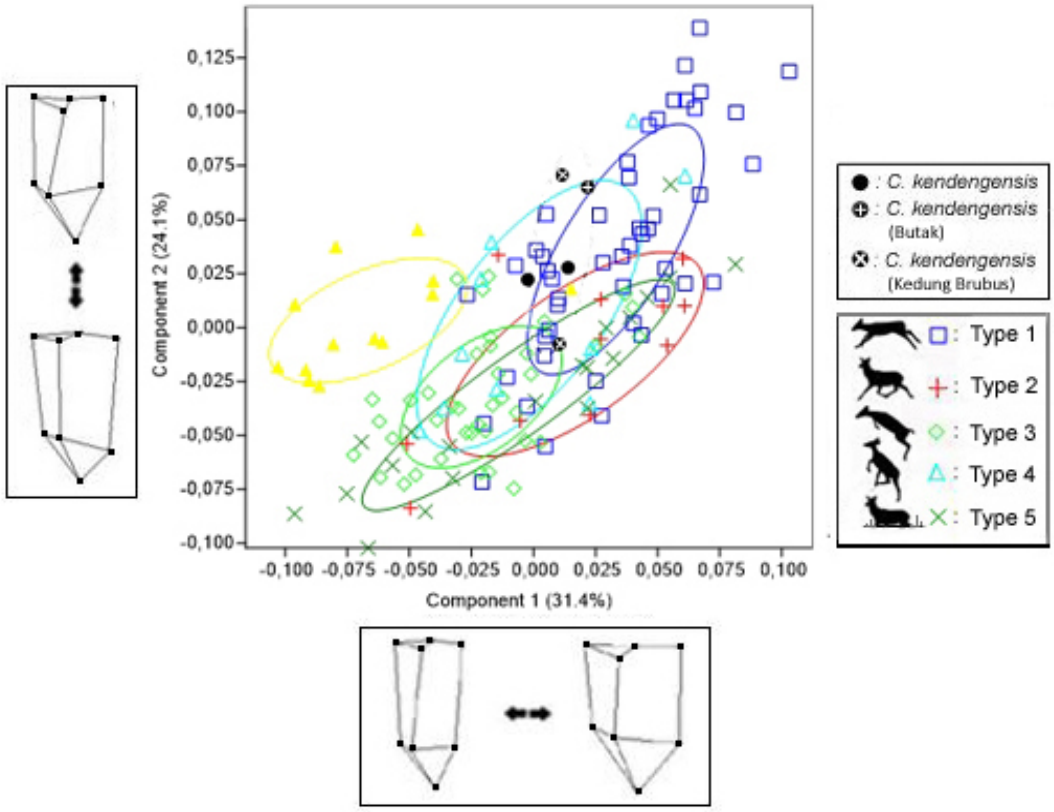


Figure 6.28: PC1 and PC2 scatterplot of a between groups PCA of all extant intermediate phalanges and Cervus kendengensis phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.

PC1	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	CKE
Type 1	-	0.2801	**<0.0001**	**0.0056**	**0.0052**	**<0.0001**	0.1662
Type 2	0.2801	-	**0.0061**	0.2751	0.2393	**0.0004**	0.4278
Type 3	**<0.0001**	**0.0061**	-	0.1764	0.3656	**<0.0001**	**0.0062**
Type 4	**0.0056**	0.2751	0.1764	-	0.676	**0.0004**	0.5815
Type 5	**0.0052**	0.2393	0.3656	0.676	-	**0.0016**	0.9729
Type 6	**<0.0001**	**0.0004**	**<0.0001**	**0.0004**	**0.0016**	-	**0.0057**
CKE	0.1662	0.4278	**0.0062**	0.5815	0.9729	**0.0057**	-
PC2	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	CKE
Type 1	-	**0.0031**	**<0.0001**	0.0819	**<0.0001**	**0.0114**	0.9879
Type 2	**0.0031**	-	0.1011	0.5495	0.1934	0.3247	0.0541
Type 3	**<0.0001**	0.1011	-	**0.019**	0.8414	**0.0004**	**0.0012**
Type 4	0.0819	0.5495	**0.019**	-	0.0556	0.6418	0.1984
Type 5	**<0.0001**	0.1934	0.8414	0.0556	-	**0.0234**	0.0108
Type 6	**0.0114**	0.3247	**0.0004**	0.6418	**0.0234**	-	**0.061**
CKE	0.9879	0.0541	**0.0012**	0.1984	**0.0108**	0.061	-

Table 6.13: p-values of Mann-Whitney pairwise comparisons of a Kruskal-Wallis test for PC1 and PC2 of the bg- PCA on all extant intermediate phalanx specimens and Cervus kendegensis fossils (CKE), with significant values ($p<0.05$) in bold.

Together the results of the Kruskal-Wallis test, the associated pairwise comparisons and the visual assessment of the PCA scatterplot, suggested that *Cervus kendengensis* had intermediate to relatively robust phalanges, a trait associated with limited capacity for splaying and preference for open environments with dry, unyielding substrates. It remains possible that *Cervus kendengensis* had phalanges that were morphologically in the range of animals adapted to intermediate environments or species of open environments with wet, yielding substrates. On the other hand, it was unlikely that *Cervus kendengensis* had phalanges similar in shape to those of species adapted to closed environments with wet substrates. Since the morphological differences summarized by PC1 were linked to the functional hypotheses proposed for the intermediate phalanx (see section 6.2.2.4), the patterns described by the *Cervus kendengensis* group were most likely ecomorphologically significant.

On the second axis the patterns described by the habitat/locomotor groups were also virtually the same as in the extant model (Fig. 6.28). This suggested that the addition of the fossil specimens did not lead to altered between-group relationships on the second axis. The visual assessment of the scatterplots showed that the fossil group gave high scores on PC2, along with the type 1 and (part of) the type 4 specimens. When PC2 was plotted against PC1 (Fig. 6.28), the *Cervus kendengensis* specimens visually clustered best with the type 1 and type 4 groups.

The Kruskal-Wallis test on the scores of PC2 indicated significant between group differences (H=53.42, p<0.0001). Pairwise comparisons (Table 6.13) for the largest part gave the same significant differences between the habitat/locomotor groups as in the extant model (see Table 6.5). Two exceptions were noted: in the *Cervus kendengensis* analysis the type 2 group was not significantly different from the type 3 group (p=0.1011) and the type 5 group was significantly different from the type 6 group (p=0.02346). The observed trends largely corroborated the observation that the fossil specimens did not alter (extant) specimen

between-group relationships to a large extent. As far as the fossil specimens were concerned; the pairwise comparisons associated with the Kruskal-Wallis test indicated that the *Cervus kendengensis* group was significantly different from the type 3 (p=0.001294) and type 5 groups (p=0.01085) on the second axis, but not from the type 1 (p=0.9879), type 2 (p=0.05412), type 4 (p=0.1984) and type 6 groups (p=0.06108). As such, the results mainly suggested a similarity between *Cervus kendengensis* and the type 1 and type 4 groups.

Taking the results of the Kruskal-Wallis test, the associated pairwise comparisons and the visual assessment of the scatterplot associated with PC2 into account, it could be concluded that the *Cervus kendengensis* phalanges were probably most similar in morphology to those of cursorial cervids adapted to open environments with dry, unyielding substrates, or –perhaps more unlikely- to those of relatively cursorial species found in high altitude environments with dry, open vegation. Morphologically this was expressed in phalanges with deep proximal articular surfaces and in a highly placed anterior extensor process. As the morphological differences summarized by the second axis were linked to the functional hypotheses proposed for the phalanx, the patterns described by the *Cervus kendengensis* specimens on this axis can be considered ecomorphologically significant.

On PC3 and PC4 visual separation between the different groups was minimal. On the third axis all groups tended to cluster in the center of the graph. The type 1 group tended to give somewhat higher scores and the type 3 and *Cervus kendengensis* group gave somewhat lower scores, but differences were too small to discern a clear pattern in the scatterplots (see Appendix M). Similarly, on PC4, there was also too much visual overlap to discern any meaningful patterns. Furthermore, the few visual separations that were observed along PC3 and PC4, were not considered particularly relevant to this ecomorphological study. As mentioned in section 6.2.1.3, the lack of meaningful patterns and the absence of a clear functional correlation for these axes in the extant model, made it doubtful that the

morphological variation explained by PC3 and PC4, and therefore the position of the fossils along these axes, was ecomorphologically significant.

In sum, it could be concluded from the analysis of the *Cervus kendengensis* phalanges, that in terms of general shape, the phalanges of this species were most comparable to those of somewhat cursorial cervids associated with open environments and wet substrate or alternatively high altitude environments. However, when specifically looking at the shape components that were thought to contain the strongest ecomorphological signals (PC1 and PC2), a similarity was suggested between the fossil phalanges and the phalanges of cursorial cervids of dry, open environments, high altitude environments or intermediate environments.

6.3.3 Sangiran

6.3.3.1 Introduction

For the analysis of Sangiran, nine calcanei from this site were added to the extant species model, resulting in a combined dataset of 134 specimens (see Tables 5.2 and 5.3). Eight of these were of the size of *Axis* and probably belonged to this genus. One specimen was of the size of *Cervus* (*Rusa*) and was also placed in this taxon (see Appendix C). Although all calcanei were part of the Grenzbank or the Upper/Lower Kabuh formation, one specimen (GMB sa170378 in Appendix C) was certainly associated with the Grenzbank. For the analysis of the intermediate phalanges, seven fossil specimens were added to the extant sample, resulting in a combined dataset of 149 specimens (see Tables 5.2 and 5.3). Four of these were of the size of *Axis* and presumably belonged to this genus and three were of the size of *Cervus* (*Rusa*) and should also be placed in this taxon (see Appendix C). All specimens were thought to belong to the Grenzbank or the Upper or Lower Kabuh formation, but one phalanx (GMB sa-nr16 in Appendix C) was definitely part of the Grenzbank.

All specimen combinations were resubmitted to a new GPA, followed by a bg-PCA on the procrustes residuals. As sample sizes for both elements were relatively small, no separate analyses were conducted on the *Cervus*- or *Axis*-sized materials that were part of the Sangiran collection. Eigenvalues and broken stick distributions were added to Appendix K.

6.3.3.2 Calcaneus

An NPMANOVA on the scores of the first four components indicated significant between group differences (F=8.81, p=0.0001). Pairwise comparisons (Table 6.14) gave the same significant differences that were also observed between the habitat/locomotion groups in the extant species model (see section 6.2.1.3). Non-significant differences were only measured between the type 2 and the type 3 specimens (p=0.2813). The Sangiran fossils did not interfere with the patterns described by the extant specimens. In addition to the extant between-group differences, the Sangiran sample was found to be significantly different from the type 1 (p=0.0005), type 2 (p=0.0058), type 3 (p=0.0001), type 4 (p=0.0014) and type 5 groups (p=0.0001) in multidimensional space. It was in other words suggested that the calcaneus specimens from Sangiran had a different morphology from that of the other species in the extant habitat/locomotor groups.

	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5
Sangiran	-	**0.0005**	**0.0058**	**0.0001**	**0.0014**	**0.0001**
Type 1	**0.0005**	-	**0.0009**	**0.0001**	**0.0026**	**0.0001**
Type 2	**0.0058**	**0.0009**	-	0.2813	**0.0155**	**0.003**
Type 3	**0.0001**	**0.0001**	0.2813	-	**0.0042**	**0.0001**
Type 4	**0.0014**	**0.0026**	**0.0155**	**0.0042**	-	**0.0001**
Type 5	**0.0001**	**0.0001**	**0.003**	**0.0001**	**0.0001**	-

Table 6.14: p-values of pairwise comparisons of an NPMANOVA of the first four PC-scores of a between groups PCA on all extant calcaneus specimens and the Sangiran fossils, with significant values (p<0.05) in bold.

The visual assessment of the scatterplot of PC1 and PC2 (Fig. 6.29) was in line with the results of the NPMANOVA and the pairwise comparisons, but provided additional insight

into the relationships between the fossils and the extant habitat/locomotor groups. Specimen distribution on PC1 confirmed the patterns found in the extant species model. Despite considerable visual overlap, type 1 and type 4 specimens gave relatively high scores, while type 3 and type 5 specimens gave lower scores. Type 2 specimens were intermediate. The fossil specimens from Sangiran gave high scores, similar to the type 1 and type 4 groups. When PC1 was plotted against PC2, the fossils primarily clustered with the type 1 group.

The patterns observed in the visual assessment of PC1 on the scatterplot were corroborated by the results of the Kruskal-Wallis test (H=48.25, p<0.0001) and the pairwise comparisons (Table 6.15). The Sangiran specimens differed significantly from the type 2 (p=0.0184), type 3 (p=0.002728) and type 5 groups (p=0.000294) on this axis. No significant differences were found between the Sangiran group and the type 1 (p=0.1973) and type 4 groups (p=0.5365).

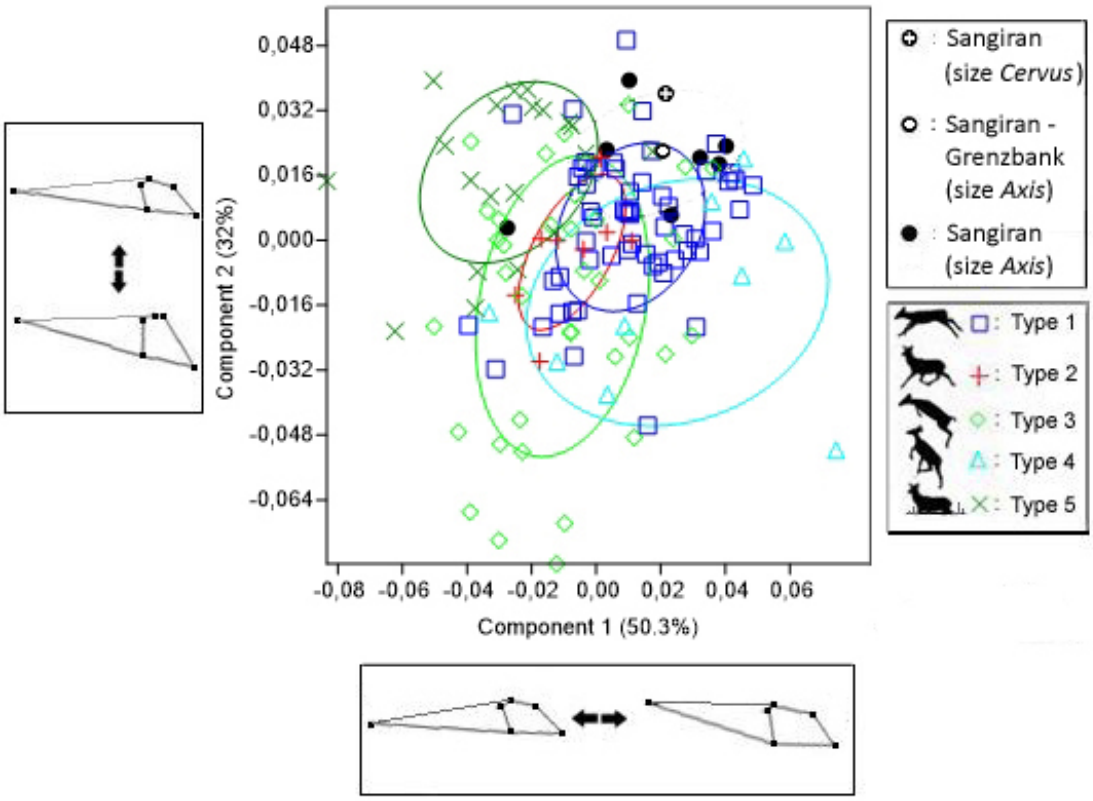


Figure 6.29: PC1 and PC2 scatterplot of a between groups PCA of all extant calcanei and fossil calcanei from Sangiran ordered by habitat/locomotor strategy with 50% confidence intervals.

PC1	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5
Sangiran	-	0.1973	**0.0184**	**0.0027**	0.5365	**0.0002**
Type 1	0.1973	-	**0.0091**	**<0.0001**	0.1973	**<0.0001**
Type 2	**0.0184**	**0.0091**	-	0.5428	**0.0485**	**0.0179**
Type 3	**0.0027**	**<0.0001**	0.5428	-	**0.0081**	**0.0223**
Type 4	0.5365	0.1973	**0.0485**	**0.0081**	-	**0.0009**
Type 5	**0.0002**	**<0.0001**	**0.0179**	**0.0223**	**0.0009**	-
PC2	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5
Sangiran	-	**0.0018**	**0.0017**	**0.0004**	**0.0019**	0.6509
Type 1	**0.0018**	-	0.3851	**0.0032**	**0.0261**	**0.0032**
Type 2	**0.0017**	0.3851	-	0.4633	0.1629	**0.0137**
Type 3	**0.0004**	**0.0032**	0.4633	-	0.9073	**<0.0001**
Type 4	**0.0019**	**0.0261**	0.1629	0.9073	-	**0.0013**
Type 5	0.6509	**0.0032**	**0.0137**	**<0.0001**	**0.0013**	-

Table 6.15: p-values of Mann-Whitney pairwise comparisons of a Kruskal-Wallis test for PC1 and PC2 of the bg- PCA on all extant calcaneus specimens and Sangiran fossils, with significant values ($p<0.05$) in bold.

Based on the Kruskal-Wallis test, the pairwise comparisons and the visual assessment of the scatterplots associated with PC1, it could be concluded that the fossil calcanei from Sangiran had a shape similar to that of cervids associated with a cursorial locomotor strategy or perhaps somewhat saltatorial strategy but with high endurance and speed, traits found in animals of open or possibly mountainous environments. Morphologically this was expressed in relatively short calcanei with a tuber that was at a higher angle relative to the anterior portion of the calcaneus (see Fig. 6.1). This was not surprising, as most cervid specimens from Sangiran were in the smaller *Axis* size class and could well belong to *Axis lydekkeri*, the species commonly found in Trinil and giving a similar result (see section 6.3.1.2). The single Sangiran specimen placed in the *Cervus* size class, did not differ in this respect and gave similar scores on the first axis. Considering that the shape variation explained by the first component was probably to a substantial extent functionally driven (see section 6.2.1), it was likely that the patterns described by the Sangiran specimens were ecomorphologically significant.

PC2 resulted in reasonably good visual separations (Fig. 6.29). Like in the extant species model, the type 1, type 2 and type 5 groups gave relatively high scores on the axis, while the type 3 group gave low scores. Contrary to the extant model, the type 4 group gave rather low scores on the axis in this case. This indicated that the addition of the fossils from Sangiran somewhat interfered with the original specimen positions on this axis. Deformation grids nevertheless showed that the same shape changes were summarized by PC2 as in the model. The fossils from Sangiran themselves gave high scores on the second axis, similar to the type 1 and type 5 groups. It should be mentioned that the single *Cervus*-sized specimen in the fossil dataset, together with one of the smaller *Axis*-sized specimens gave exceedingly high scores on the axis. When PC2 was plotted against PC1 the fossils clearly clustered with the type 1 group, but not the type 5 group.

The observed between group-differences were partially confirmed by the Kruskal-Wallis test ($H=35.07$, $p<0.0001$) and the associated pairwise comparisons (Table 6.15). Separations were better supported in this analysis than in the analysis of the extant species (see Table 6.3), again indicating that the addition of the Sangiran specimens to some extent interfered with the original patterns described by PC2 in the model. The shape changes explained by this axis were, nevertheless, the same as in the model. The pairwise comparisons furthermore indicated that the Sangiran group was significantly different from the type 1 ($p=0.001806$), type 2 ($p=0.001764$), type 3 ($p=0.000431$) and type 4 groups ($p=0.001998$). No significant differences were, on the other hand, found between the Sangiran group and the type 5 group ($p=0.5609$), perhaps implying the fossil group was most similar to this habitat/locomotor group on the second axis.

Considering the results of the Kruskal-Wallis test, the associated pairwise comparisons and the visual assessment of the second axis in the scatterplot, it could be concluded that the Sangiran calcanei had relatively long articular surfaces supporting the malleolus. This was

especially the case for the single *Cervus*-sized specimen. Such a trait is unlikely to be found in saltatorial animals associated with closed environments and wet substrates. As far as the articular surface supporting the malleolus was concerned, the Sangiran specimens were morphologically similar to more cursorial species, or at least intermediate forms, associated with either dry or wet open environments, or high altitude environments.

PC3 and PC4 (Appendix L) only resulted in limited visual separation. On the third axis all specimens tended to give intermediate scores and clustered in the center of the plot. Only the type 2 specimens, together with the Sangiran specimens, gave somewhat lower scores. These separations were confirmed by the Kruskal-Wallis test and the pairwise comparisons (Appendix L). Similarly, PC4 also resulted in little visual separation in the scatterplot (Appendix L). All habitat/locomotor groups, as well as the specimens from Sangiran, tended to cluster in the center of the plot. The analysis of the extant specimens already suggested that the shape differences explained by the second and fourth axes of variation lacked a clear functional correlation with locomotor strategy and substrate/vegetation type (see section 6.2.1.3). Consequently, specimen distribution along PC3 and PC4 was probably of limited ecomorphological significance.

In conclusion, it could be stated from the results of the Sangiran analysis that the calcanei from this site were, in terms of general shape, most similar to those of intermediate environment species on a gradient between cursorial forms of dry, open environments and saltatorial forms of wet, closed environments. However, when specifically looking at those traits that were considered to contain the strongest ecomorphological signal (PC1 and PC2), the calcanei were morphologically much more similar to those of species with a cursorial locomotor strategy, associated with dry, open environment, potentially of high altitude (PC1 and PC2). The shape of the calcanei was also to a lesser extent somewhat similar to that of open, wet environment species (PC2).

6.3.3.3 Intermediate phalanx

The results of the NPMANOVA on PC1 to PC4 indicated significant between group differences (F=13.71, p=0.0001). P-values calculated in the pairwise comparisons (Table 6.16) largely mirrored the significant differences between the habitat/locomotion groups in the extant species model. The only difference was that in the model the type 4 group was significantly different from the type 5 group (see Table 6.4), but that this was not the case in the Sangiran analysis (p=0.1115). This implied that the addition of the Sangiran fossils led only to limited interference in the patterns described by the different groups in the model. The Sangiran sample itself was significantly different from the type 1 (p=0.0041), type 3 (p=0.0001) and type 6 groups (p=0.0001), but not from the type 2 (p=0.0742), type 4 (p=0.0939) and type 5 groups (p=0.0518).

	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Sangiran	-	**0.0041**	0.0742	**0.0001**	0.0939	0.0518	**0.0001**
Type 1	**0.0041**	-	**0.0075**	**0.0001**	**0.0087**	**0.0001**	**0.0001**
Type 2	0.0742	**0.0075**	-	**0.0019**	0.56	0.0736	**0.0003**
Type 3	**0.0001**	**0.0001**	**0.0019**	-	**0.0154**	**0.008**	**0.0001**
Type 4	0.0939	**0.0087**	0.56	**0.0154**	-	0.1115	**0.0048**
Type 5	0.0518	**0.0001**	0.0736	**0.008**	0.1115	-	**0.0013**
Type 6	**0.0001**	**0.0001**	**0.0003**	**0.0001**	**0.0048**	**0.0013**	-

Table 6.16: p-values of pairwise comparisons of an NPMANOVA of the first four PC-scores of a between groups PCA on all extant intermediate phalanges and the Sangiran fossils, with significant values (p<0.05) in bold.

The visual assessment of the scatterplot associated with the first two components (Fig. 6.30) was largely in line with the results of the NPMANOVA, but gave further insight into the between-group relationships of the extant groups and the fossil specimens along the principal component axes. Along PC1 (Fig. 6.30), the same patterns were observed between the habitat/locomotor groups as in the extant model. As a group, the Sangiran specimens were probably closest to the intermediate the type 2 group. When looking at the specimens

individually it appeared that the *Axis*-sized fossils gave scores in the range of the type 3 and type 5 groups, while the *Cervus*-sized fossils gave lower scores, similar to the type 1 group.

The Kruskal-Wallis test on the scores of PC1 gave significant between group differences (H=63.39, p<0.0001). Pairwise comparisons (Table 6.17) mirrored the between group-differences measured between the habitat/locomotor groups in the extant species model. The only exceptions were that in the Sangiran analysis, the type 1 group differed significantly from the type 2 group (p=0.03642) and the type 6 group was not significantly different from the type 3 (p=0.1003) and type 5 groups (p=0.2171), like in the model. The fossils (as a group) differed significantly from the type 3 (p=0.001068) and type 6 groups (p=0.002602), but not from the type 1 (p=0.1687), type 2 (p=0.8563), type 4 (p=0.204) and type 5 groups (p=0.2806), confirming a possible closeness of the Sangiran group to the type 2 group.

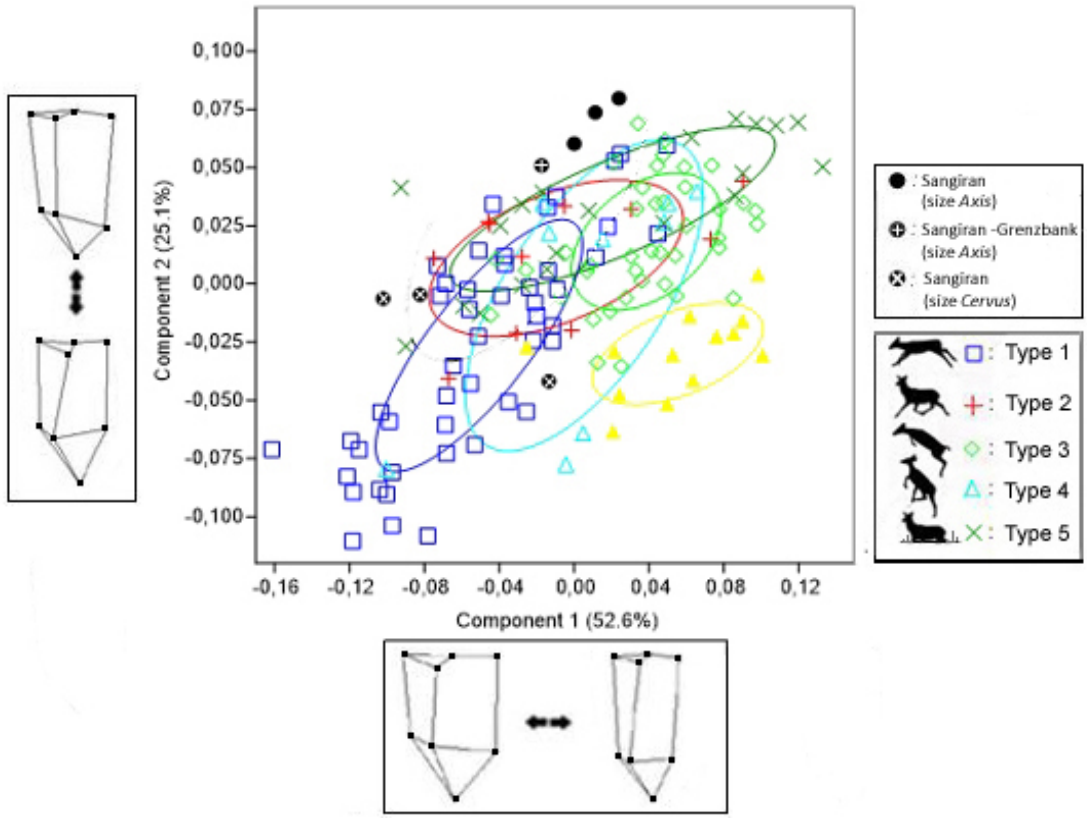


Figure 6.30: PC1 and PC2 scatterplot of a between groups PCA of all extant intermediate phalanges and Sangiran phalanges, ordered by habitat/locomotor strategy with 50% confidence intervals.

PC1	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Sangiran	-	0.1687	0.8563	**0.001**	0.204	0.2806	**0.0026**
Type 1	0.1687	-	**0.0364**	**<0.0001**	**0.003**	**0.0003**	**<0.0001**
Type 2	0.8563	**0.0364**	-	**0.0046**	0.3619	0.2562	**0.0076**
Type 3	**0.001**	**<0.0001**	**0.0046**	-	0.0648	0.4193	0.1003
Type 4	0.204	**0.003**	0.3619	0.0648	-	0.832	**0.0162**
Type 5	0.2806	**0.0003**	0.2562	0.4193	0.832	-	0.2171
Type 6	**0.0026**	**<0.0001**	**0.0076**	0.1003	**0.0162**	0.2171	-
PC2	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Sangiran	-	**0.0128**	0.3191	0.4285	0.1688	0.7609	**0.0089**
Type 1	**0.0128**	-	**0.0099**	**<0.0001**	0.1339	**<0.0001**	0.6534
Type 2	0.3191	**0.0099**	-	0.5592	0.9394	0.0603	**0.0011**
Type 3	0.4285	**<0.0001**	0.5592	-	0.6237	0.0831	**<0.0001**
Type 4	0.1688	0.1339	0.9394	0.6237	-	0.0771	0.2045
Type 5	0.7609	**<0.0001**	0.0603	0.0831	0.0771	-	**<0.0001**
Type 6	**0.0089**	0.6534	**0.0011**	**<0.0001**	0.2045	**<0.0001**	-

Table 6.17: p-values of Mann-Whitney pairwise comparisons of a Kruskal-Wallis test for PC1 and PC2 of the bg- PCA on all extant intermediate phalanx specimens and Sangiran fossils, with significant values ($p<0.05$) in bold.

In sum, the Kruskal-Wallis test, the associated pairwise comparisons and the visual assessment of the scatterplots associated with PC1 indicated that the Sangiran specimens, as a group, had a morphological signature typical of intermediate species on a gradient between cursorial species of dry, open environments with more robust phalanges and saltatorial species of wet, closed environments with more gracile phalanges. Yet, there appeared to be a dichotomy in the fossil sample and the *Axis*-sized specimens were more similar in shape to somewhat cursorial species of open, wet environments with more gracile phalanges, while the *Cervus*-sized specimens were more robust and similar to forms typical of dry, open environments. As the morphological traits associated with PC1 were considered functionally correlated, it is assumed that the patterns described by the fossils on this axis, were ecomorphologically significant.

On PC2, the patterns visually observed in the Sangiran analysis (Fig. 6.30) were largely the same as in the extant model. The type 1 and type 4 specimens gave more negative scores

while the type 3 and type 5 specimes gave more positive scores. The fossil specimens, on average, seemed to give intermediate scores on the second axis, similar to the type 2 group. Like on the first axis, there also appeared to be a difference between the *Axis*-sized specimens, that gave high scores, similar to the type 5 group, and the *Cervus*-sized specimens, that gave lower scores, similar to the type 1 group.

The patterns observed in the visual assessment of the scatterplot associated with PC2 were partially confirmed by the results of the Kruskal-Wallis test (H=46.2, p<0.0001) and the pairwise comparisons (Table 6.17). The addition of the Sangiran specimens to the extant species sample altered the original patterns between the habitat/locomotor groups to some extent. In addition to the significant differences observed on PC2 in the model (see Table 6.5), the type 6 group was in the Sangiran analysis also significantly different from the type 2 (p=0.001177) and type 5 groups (p<0.0001), but not from the type 1 group (p=0.6534). The type 3 group was also not significantly different from the type 2 (p=0.5592) and the type 4 group (p=0.6237). The Sangiran fossils, as a group, were significantly different from the type 1 (p=0.01286) and type 6 groups (p=0.008922), but not from the type 2 (p=0.3191), type 3 (p=0.4285), type 4 (p=0.1688) and type 5 groups (p=0.7609) on the second axis. This implied that the Sangiran specimens were morphologically different from the type 1 and type 6 groups and possibly similar to the type 2 group, but also to the type 3 group and the type 5 group.

The visual assessement of the scatterplot associated with PC2, the results of the Kruskal-Wallis test and the associated pairwise comparisons suggested that the Sangiran phalanges morphologically conformed to those of intermediate cervids on a gradient between cursorial species of dry, open environments and saltatorial species of wet, closed environments, or alternatively to somewhat cursorial species of wet, open environments. In reality the results most likely reflected the same dichotomy between the *Cervus*-sized specimens and *Axis*-sized specimens, also observed along PC1. The smaller *Axis*-sized deer seemed to belong to a

morphotype characterized by relatively shallow proximal articular surfaces and a low placement of the extensor process on the anterior side of the phalanx, traits typical of species adapted to environments with wet, yielding substrates. The larger *Cervus*-sized specimens appeared to be of a morphotype characterized by relatively deep proximal articular surfaces and a high placement of the extensor process on the anterior side of the phalanx, both traits typical of cursorial species adapted to environments with dry substrates. From the extant model it was concluded that the morphological variation summarized by PC2 was functionally correlated. The patterns described by the Sangiran specimens on this axis should therefore be considered ecomorphologically significant.

PC3 and PC4 were retained as relevant components as they explained a substantial amount of real shape variance in the PCA (see Appendix M). On PC3 separations did not result in any meaningful patterns from an ecomorphological perspective. Most specimens tended to cluster in the center of the graph. Only the type 6 group and the Sangiran specimens gave somewhat more positive scores on the axis, a pattern that was confirmed by the Kruskal-Wallis test and the associated pairwise comparisons (Appendix M). On PC4, separations were even more limited, with only the type 5 group giving somewhat more positive scores (Appendix M). The extant species analysis, however, indicated that the morphological variation along the third and fourth axes was not strongly functionally correlated. The ecomorphological significance of these shape components was therefore probably limited.

In summary, the results of the analysis revealed that the phalanges from Sangiran were, in terms of general shape, most similar to those of intermediate cervids on a gradient between cursorial forms of dry, open environments and saltatorial forms of wet, closed environments, or somewhat cursorial forms associated with high altitude environments. When looking specifically at the shape components with the strongest ecomorphological signal (PC1 and PC2) a morphological similarity to the intermediate species was confirmed, but a difference

was noted between the *Axis*-sized and *Cervus*-sized specimens, the former being more similar in shape to species of open or closed environments with a wet substrate, the latter being more similar in shape to species of dry, open environments.

7. Discussion

7.1 Introduction

This dissertation had multiple objectives. A first goal was to construct ecomorphological methods for the cervid calcaneus and intermediate phalanx that allow for predictions to be made about fossils of unknown ecological affinity. This involved exploring a number of functional hypotheses related to these two elements (see section 5.2) and assessing the effectiveness of certain morphological traits in predicting ecological parameters. The second goal, was to apply these newly developed methods on fossils from several Javan hominin sites to: A) assess past environmental conditions at *Homo erectus* localities, B) detect any differences/changes in these environmental conditions through time and space, C) determine to what extent *Homo erectus* was associated with a specific type of environment or was able to adapt to changing conditions, and D) evaluate how the findings relate to current models about hominin dispersal.

In this chapter I discuss how these goals have been reached and how the results presented in chapter 6 fit with evidence from other studies and proxies pertaining to the above outlined research problems. More specifically, section 7.2 builds on the results of the extant and fossil analyses (see sections 6.2 and 6.3) and discusses the utility of the ecomorphological methods presented here and how they relate to earlier, similar studies. In section 7.3, the results of the fossil analyses are integrated and discussed in connection with other palaeoenvironmental studies from the examined sites and the region. Section 7.4 deals with the contributions of these habitat reconstructions in the broader context of hominin palaeoecology and discusses the wider implications for early *Homo erectus* dispersal in Southeast Asia and further afield. A final section 7.5 gives some further consideration to some of the statistical tests that were used in this study and the implications for the results.

7.2 Cervid ecomorphology

Developing postcranial ecomorphological models to predict extinct species' habitat preferences was fundamental to this dissertation. Consequently, it was imperative to first consider the utility of the specific models developed. The best way to estimate the effectiveness of a skeletal element in predicting habitat preference is to look at how extant specimens of known ecological affinity "behave" in a predictive model and at the underlying reasons for certain anatomical patterns to manifest themselves in morphospace (Curran 2009, Barr 2014).

Many similar ecomorphological studies have made use of Linear Discriminant Analyses (LDA) (e.g. Bishop 1994, Kovarovic & Andrews 2007, Plummer & Bishop 1994, Plummer *et al.* 2008) and have correspondingly looked at reclassification rates to assess model effectiveness. As this dissertation made use of between groups PCA as an alternative for the informed LDA method (i.e. a method where pre-assigned groups drive separations), evaluating the success of the models isn't as easy as comparing the success rates of the correctly predicted individuals in an LDA. The effectiveness of a given element to predict habitat preference was assessed here in another way (see below) and the results were therefore more difficult to directly compare to those of LDA-based studies. That being said, problems of comparison are not unique to this dissertation, as a wide range of different methods (e.g. different sets of linear measurements or GMM landmarks, different numbers and types of habitat categories) have been reported in the artiodactyl ecomorphological literature (see e.g. Kappelman 1988, Plummer & Bishop 1994, Degusta & Vrba 2003, 2005a, 2005b, Scott 2004, Plummer *et al*. 2008, Schellhorn 2009, Barr 2014a).

Emphasis was placed on the functional aspects underlying morphological variation, so the effectiveness of a predictive model was estimated by how well a proposed functional

hypothesis fitted with the results of the analyses. The deformation grids associated with the individual axes of the PCA (see section 6.2) proved useful for this. When the morphological variation explained by the deformation grid of a specific axis was in line with the shape differences that were predicted to be functional, this was taken as an indication for a correlation between shape and locomotor strategy/ecological affinity. The placement of specimens along the axis, the statistical significance of separations between the groups and the extent to which the patterns could be reconciled with the proposed hypotheses, were used to assess the presence of a functional signal.

Calcaneus

In Chapter 5 three functional hypotheses were proposed for the calcaneus, a summary of which can be found in Figure 7.1. Morphological traits predicted to be ecomorphologically significant, were the length of the tuber calcanei, the orientation of the articular facets between the calcaneus and astragalus and between the calcaneus and cubonavicular, and the size of the articular surface supporting the malleolus (see full explanations in section 5.2).

The first two hypotheses were confirmed by the patterns displayed along the first axis of the PCA and by the associated deformation grids. As explained in chapter 6, the shape variation of this axis reflected a gradient from saltatorial species of wet, closed environments (type 3) with long, horizontally placed tuber calcanei to cursorial species of dry, open environments (type 1), with short, vertically placed tuber calcanei. These differences were statistically significant (see section 6.2.1.3) and suggested that the model effectively differentiated between species of dry, open environment and wet, closed environment.

Calcaneus	Explanation	Confirmed/not confirmed	Morphotype A	Morphotype B
Hypothesis 1:	The relative length of the tuber calcanei is predicted to be greater in species adapted to closed environments (A) and shorter in species adapted to open environments (B).	Confirmed (PC1)		
Hypothesis 2	The orientation of the articular facets between calcaneus and cubonavicular and between calcaneus and astragalus is predicted to be more oblique in species adapted to more open environments (B) and less oblique in species of closed environments (A).	Confirmed for the articular facet between the calcaneus and the astragalus (PC1), but not for the articular facet between the calcaneus and the cubonavicular.		
Hypothesis 3	The articular surface supporting the malleolus is predicted to be larger in species adapted to open environments (B) and shorter in species adapted to closed environments (A).	Confirmed (PC2)		

Figure 7.1: Summary of the results of the extant calcaneus model, with proposed functional hypotheses and drawings of morphotypes (shaded regions represent features relevant to functional hypotheses).

The fact that morphological variation in the length and orientation of the tuber were summarized together by the same axis indicated a close (functional) relationship between the two traits, as predicted in the functional hypotheses. Intermediate species (type 2) gave values in between these two opposites and had tuber calcanei of intermediate length and with an orientation that was neither as vertically placed as in those of cursorial species, nor as horizontally placed as in those of saltatorial species. Although the intermediate group had a transitional shape, overlap with the wet, closed environment group was substantial. Accordingly, the model did not discriminate as well between intermediate and wet, closed environment species.

Despite being predicted in the functional hypotheses, variation in the orientation of the articular surface with the cubonavicular was not observed. This was, no doubt, a methodological issue. Although an attempt was made to define a landmark on the anterior end of this facet, as a way to account for the morphology of this part of the bone, preliminary tests revealed that no easily repeatable homologous landmarks were found there. It was therefore difficult to adequately register variation in this morphological trait using the GMM protocol.

The separately treated mountain species (type 4) and open wetland species (type 5) proved somewhat more difficult to interpret. The calcanei of mountain adapted species had tuber calcanei that were of the same length and orientation, as those of species of dry, open environments. As indicated before (section 6.2.1.3), this may be because none of the extant deer are true mountain species. Most cervids found at high altitudes are adapted to locomotion on relatively flat (often open) terrain (Geist 1998). That being said, certain bovids are more adapted to true mountain environments (e.g. *Capra ibex* and *Hemitragus jemlahicus*), but even in the Bovidae family the addition of a mountain category in ecomorphological analyses, has not proven to be of much use for the calcaneus and astragalus (Kovarovic 2004, Weinand 2005, 2007). In these studies type 4 specimens were misclassified into other habitat categories

and substantially overlapped with other groups. A plausible explanation for this is that the morphology of the calcaneus and astragalus in mountain species is probably more driven by vegetation structure than by altitude or the gradient of the slope. In the relatively open environments in which most "mountain" cervids are found, a cursorial evasion strategy may be most optimal. The statistically significant differences (see section 6.2.1.3) measured between the mountain group and the other habitat/locomotor groups confirmed that the model could effectively differentiate this group on the shape of the tuber, but that there was a similarity to the dry, open environment species, who employ cursorial locomotion in avoiding prey.

In the functional hypotheses proposed for the calcaneus (section 5.2) the emphasis was placed on the idea that the morphology of the calcaneus was mainly driven by differences in vegetation structure. Although not strictly a vegetational parameter, due to the specificity of wetland environments there was, nevertheless, a distinction made between species adapted to dry environments with an open vegetation and species adapted to wet environments with an open vegetation. The results of the ecomorphological analyses showed that calcanei of species of wet environments with open vegetation (type 5) had tuber calcanei, and a general orientation, similar to those of taxa associated with a closed vegetation structure. As previously suggested (section 6.2.1.3), this could be because the specific vegetation structure of such open wetlands has characteristics more similar to the vegetation structure found in closed vegetation habitats. A plausible explanation is offered by Curran (2009), who argued that the open wetlands inhabited by type 5 forms, are usually dominated by tall grasses and reeds that provide more cover than the truly open landscapes inhabited by cursorial forms. Such obstacles in the landscape require a more saltatorial strategy for evading predators.

The third functional hypothesis for the calcaneus was confirmed by specimen patterns along the second component in the PCA and by the associated deformation grids (section 6.2.1.3).

The shape variation explained by PC2 showed variation in the relative size of the articular surface supporting the malleolus on a gradient from dry, open species (type 1) with relatively long articular surfaces supporting the malleolus, to wet, closed habitat species (type 3) with relatively short articular surfaces supporting the malleolus. These differences were statistically significant (section 6.2.1.3) and suggest that the model can effectively differentiate between species of open environments and closed environments. Intermediate specimens (type 2) were morphologically in between these two extremes, but more similar to the closed environment group.

The mountain species (type 4) were morphologically analogous to cursorial species of dry, open environments, further confirming the interpretation that the (functional) morphology of the calcaneus in such species is driven more by vegetation structure than by altitude (see explanation above). The relatively long articular surface supporting the malleolus in mountain species suggests a reliance on cursoriality and that such species are probably more adapted to relatively flat, open terrain at high altitude (Geist 1998).

The open wetland morphotype (type 5) was more difficult to interpret, as the results are at odds with the second functional hypothesis (see section 6.2.1.3). When looking at the length and orientation of the tuber calcanei (second hypothesis), this group is similar to cervids of wet, closed environments. However, the shape of the articular surface supporting the malleolus was typical of dry, open environment species. The reason for this discrepancy was unclear, but it seems that cervids adapted to open wetlands also retain some cursorial traits. That being said, the length and orientation of the tuber calcanei were, in all probability, the more important morphological traits (i.e. explaining a larger proportion of the shape variance, see section 6.2.1.3) and better discriminators between habitat/locomotor groups. The unexpected shape of the articular surface for the malleolus in open wetland species, could,

nevertheless, indicate that stability in the hock joint, when running at high speed, was more important in this group than in species of wet, closed environment.

Intermediate phalanx

For the intermediate phalanx five functional hypotheses were proposed (see section 5.2). Morphological traits predicted to be ecomorphologically significant, were: the depth of the proximal articulation, the antero-posterior length of the plateau postarticulaire, the height to which the anterior extensor process and the palmar extensions are extended in the proximal direction, the shape and position of the apex on the distal articulation and the overall relative length and gracility of the intermediate phalanx (Fig. 7.2).

The first and (in part) the third functional hypotheses were confirmed by the patterns displayed along the second axis of the PCA and by the associated deformation grids. The shape variation of this axis reflected a gradient from cursorial species of dry, open environments (type 1), with deep proximal articulations and anterior processes further extended in the proximal direction, to saltatorial species of wet, closed environments (type 3), with shallow proximal articulations and anterior processes less far extended in the proximal direction (Fig. 7.2). The observed differences were statistically significant (see section 6.2.1.3) and it can be concluded that the model effectively differentiated between the two ecological extremes. For the predicted relationship between the placement of the posterior palmar extentions and habitat preference/locomotor behaviour (also part of hypothesis 3), there was only limited support. Variation in this morphological trait was only observed along PC3, where between group separations where not statistically significant and no clear visual patterns were observed in the scatterplots (see section 6.2.2.4). This trait was probably not strongly driven by functional differences.

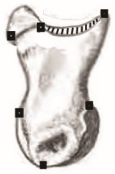
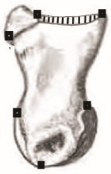
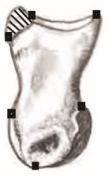
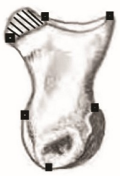
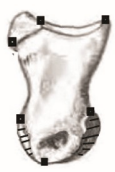
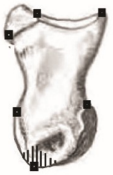
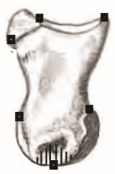
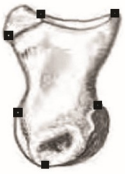
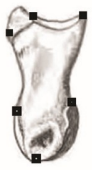
Intermediate phalanx	Explanation	Confirmed/not confirmed	Morphotype A	Morphotype B
Hypothesis 1	The proximal articulation of the intermediate phalanx is predicted to be deeper or more concave in species adapted to drier, more open environments (A), and shallower in species of wet, closed environment (B).	Confirmed (PC2)		
Hypothesis 2	The plateau postarticulaire of the intermediate phalanx is predicted to be shorter in species adapted to dry, more open environments(A) and longer in species of wet, closed environments (B).	Not confirmed		
Hypothesis 3	The extensor process on the anterior side and the palmar extensions on the posterior side of the distal articular surface of the intermediate phalanx are predicted to be further extended in species adapted to more open/drier environments(A). They are predicted to be less far extended in species of wet, closed environments (B).	Partially confirmed (variation in extensor process confirmed in PC2, variation in height palmar extensions partially confirmed in PC3)		
Hypothesis 4	The shape of the distal articular surface of the phalanx is predicted to be round on the medial and lateral side in species adapted to closed or wet environments (B) and characterized by a posterior apex on the medial side in forms adapted to open environments (A).	Not confirmed		
Hypothesis 5	The general shape of the intermediate phalanx is predicted to be more gracile/robust in species adapted to wet/closed or open/dry environments (A/B).	Confirmed, but relationship not well understood (PC1)		

Figure 7.2: Summary of the results of the extant intermediate phalanx model, with proposed functional hypotheses and drawings of morphotypes (shaded regions represent features relevant to functional hypotheses).

Intermediate species (type 2) gave scores that were in between those of dry, open forms and those of wet, closed forms and had proximal articulations of an intermediate shallowness and an intermediately placed extensor process on the anterior side. The intermediate group differentiated well from the saltatorial species of wet, closed environments, as well as from the cursorial species of open, closed environments.

It should be remembered that for the intermediate phalanx, two mechanisms were proposed that could play an important role in the functional morphology of this element: the splaying of

the phalanges and the development of morphological accommodations to increase the "pogostick effect" in the lower leg (see section 5.2). In this context the deeper proximal articulations observed in species of open, dry environments could only be explained as an adaptation to restrict medio-lateral movement (splaying) in the phalanges, as a means to increase stability when running on firm, dry substrates (Köhler 1993). The further placement of the extensor process in the proximal direction can, on the other hand, better be explained as an adaptation to increase the "pogostick effect", as this would allow for further antero-posterior flexion and extension of the phalanx (Leinders 1979). It can therefore be concluded that both mechanisms played a role in driving the shape of the intermediate phalanx.

Like for the calcaneus, the results of the intermediate phalanges from wet, open environments, mountainous environments and tundra environments needed some further contextualization. The phalanges from wet, open environments (type 5), as predicted, were of a morphotype similar to that of saltatorial species of wet, closed environment (type 3): a more shallow proximal articulation and an extensor process that was less far extended in the proximal direction. This was in accordance with functional hypotheses 1 and 3, as the shape of the phalanx was predicted to be mainly driven by substrate type and less by vegetation structure.

The separately treated tundra group (type 6) was predicted to be of a morphotype similar to that of species of wet, yielding substrate (type 3), as their shape supposedly accommodates to the more yielding nature of tundra: alternating frozen and thawing soil (Hildebrand 1985, Nieminen 1990). In practice, this group was more intermediate in shape, as far as the extensor process and the proximal articulation are concerned. Tundra species (i.e. *Rangifer tarandus*) did not have an exceptionally high or low placement of the anterior extensor process and the depth of the proximal articulation was not unusually shallow or deep. Although the results for this group did not contradict functional hypotheses 1 and 4, the more intermediate shape of the phalanx may indicate that animals found in tundra environments, perhaps in part,

accommodate their phalangeal morphology differently to this type of yielding environment, than animals found on wet substrate.

The phalanges of species found in mountainous environments (type 4) were similar to those of species found on drier substrate, but overlapped substantially with most groups. It appeared that altitude did not play a large role in driving the shape of the bone. Species that were found on dry substrate at high altitude, were of a morphotype similar to species of dry substrate at low altitude (type 1). Species found on wet substrate at high altitude were of a morphotype similar to other species adapted to wet substrates.

Although the relationships between shape and function were not as well defined for the fifth functional hypothesis, it was predicted that the gracility of the intermediate phalanx was probably also ecomorphologically correlated. Köhler (1993) proposed that the intermediate phalanx is more robust in species of wet, closed environment, but Degusta and Vrba (2005b) - despite using similar species in their study- stated that the phalanges of taxa found on wet, swampy terrain are more gracile. From the results presented in this thesis it was clear that a large part of the shape variation measured between the phalanges, were a function of gracility (summarized by PC1, see section 6.2.2.4). The shape variation along this axis reflected a gradient from cursorial species of dry, open environment (type 1) with robust phalanges, to saltatorial species of wet, closed environment (type 3) with gracile phalanges. Species with intermediate habitat preferences and locomotor strategy had an intermediate shape on the gradient. This confirmed the pattern predicted by Degusta and Vrba (2005b), and was somewhat at odds with that of Köhler (1993). Degusta and Vrba (2005b) did not provide specific functional explanations for the gracility in the phalanx and interpreting the observed variation in this trait is not straight forward. However, as in the first and fourth functional hypotheses, shape variation was primarily explained as the result of; either a difference in development of the "pogostick effect" (Leinders 1979) or a difference in the capacity to splay

the phalanges (Köhler 1993), this is probably also the case for the fifth functional hypothesis. Considering the fact that longer, more gracile phalanges were apparently connected with wet substrates (Degusta & Vrba 2005b, this study), it is not unlikely that this trait is also an accommodation that allows for a better grip on yielding substrate types.

The shape of the phalanges from wet, open (type 5), mountainous (type 4) and tundra environments (type 6) generally corroborated the confirmation of the fifth functional hypothesis. In these three groups, substrate type was also the primary driver of shape variation, certainly more so than vegetation structure. In this light, the intermediate phalanges of species associated with wet, open environments were of a more gracile morphotype, similar to that of saltatorial species of wet, closed environment (type 3). The yielding nature of substrates found in habitats such as floodplains, wet grasslands and swamps most likely played an important role.

Similar to the placement of the extensor process (hypothesis 3) and the depth of the proximal articulation (hypothesis 1), the gracility of the intermediate phalanx (hypothesis 5) was evidently also primarily driven by substrate type, and much less by the altitude at which a species is found. The phalanges of mountain species morphologically overlapped with those of species found in other habitats, but were, generally speaking, of a morphotype most similar to that of species adapted to dry substrate (type 1). This was probably the case because most mountain species included in the study were associated with a relatively dry substrate at high altitude. Species found on wet substrates at high altitude, tended to be morphologically more similar to forms associated with wet substrates of low altitude (types 3 and 5).

The tundra species (type 6) were predicted in the functional hypotheses to display a shape similar to that of species found on wet substrate (type 3). Although the placement of the extensor process and the depth of the proximal articulation (hypothesis 1 and 3) were more intermediate than expected, the tundra phalanges confirmed this and were of a similar

gracility as those of species associated with wet substrates. This confirmed the fifth functional hypothesis and the idea that reindeer have phalanges that are morphologically accommodated to the more yielding nature of tundra substrate when it thaws and refreezes (Hildebrand 1985, Nieminen 1990). It is likely that the more gracile intermediate phalanges in reindeer allow for an increased capacity for phalangeal splaying. However, the fact that these morphological accommodations to yielding substrate seemed to be mainly expressed in the overall gracility of the phalanx, and less so in the shape of the articulations, confirmed the unique shape and idiosyncratic adaptations of the reindeer phalanx.

Two other functional hypotheses were proposed for the intermediate phalanx: one related to the shape of the plateau postarticulaire (hypothesis 2) and a second one related to the shape of the distal articular surface (hypothesis 4) (see Fig. 7.2). There were no clear indications from the ecomorphological analyses that could confirm these functional hypotheses. The shape of the plateau postarticulaire and the distal articular surface were not functionally correlated and these characters were not good predictors of locomotor strategy and habitat preference.

Implications and confounding factors

As far as the calcaneus was concerned, the results were in line with those of earlier GMM-based models developed for this element (Curran 2009, 2012, 2015). Using an LDA-approach, the calcaneus resulted in high reclassification rates and generally performed quite well as a habitat predictor (Curran 2009, 2012, 2015). In contrast, studies of *bovid* ecomorphology have been less unanimous in their estimation of the calcaneus as a good habitat predictor (Kovarovic 2004, Kovarovic & Andrews 2007, Schellhorn 2009, Schellhorn & Pfretzschner 2015, Barr 2018). While some have merely urged for caution when interpreting its morphological traits (Barr 2018), others have considered it a weaker element for palaeoenvironmental inference (Kovarovic 2004, Kovarovic & Andrews 2007). The underlying reasons for this lower performance of the calcaneus are illusive, but Kovarovic

(2004) attributed misclassifications in her models to the unique morphologies present in certain forms and to phylogenetic relatedness between species. Barr (2018), who did a more detailed study of the functional morphology of the calcaneus, considered it a useful habitat predictor, but also warned for the confounding effects of allometry and phylogeny.

Despite reservations in the bovid ecomorphology literature, the model presented in this thesis is subject to limited confounding effects from phylogeny and allometry in the functionally correlated components (PC1 and PC2). The regressions of shape against log centroid size indicated that only a small degree of the shape variance explained by these components could be attributed to an allometric effect. This was in line with the observation by Biewener (1989) that in most mammals between 0.1 and 300 kg, against expectation, limb bones tend to scale more isometrically than expected. Although there were indications from the PGLS that phylogeny did play a role in driving the shape of the calcaneus, from the assessment of the (taxonomically re-ordered) PCA scatterplots it was clear that this signal was subordinate to a functional signal in the first two components (see section 6.2.1.3).

Why this study as well as Curran's (2009, 2012, 2015) cervid models have registered a weaker confounding effect from allometry and phylogeny than some bovid studies (Kovarovic 2004, Kovarovic & Andrews 2007, Barr 2018), is unclear. It could suggest a discrepancy between cervids and bovids, but could also be the consequence of methodological differences (e.g. GMM versus linear measurements). In this context it is worth noting that in Barr's (2018) bovid analyses the primary shape variations in the calcaneus were practically identical to those in the model presented here: variation in the length of the tuber calcanei, variation in the size and shape of the articular surface supporting the cubonavicular (not tested here) and variation in the articular surface supporting the astragalus. Where the latter two traits were considered mainly functional by Barr (2018), it was purported that the length of the tuber was more confounded by body size and phylogenetic relatedness (Barr 2018).

One possible explanation is that in bovids the larger species are driving the allometric signal. Cervids -with the exception of *Alces alces*- normally do not exceed the 300 kg boundry (Geist 1998), below which most mammals scale relatively isometrically (Biewener 1989). In bovids, on the other hand, many larger forms exist (e.g. *Syncerus*, *Bos*, *Taurotragus*) that may require additional morphological accommodations to support their weight (Scott 1979). Moreover, some of these large species are probably too heavy to benefit from saltatorial adaptations (e.g. the longer tuber calcanei) and could therefore obscure the functional signal (Geist 1998). Although some morphological studies (Scott 1979, Plummer & Bishop 2008) have *a priori* excluded very heavy species from their analyses for precisely these reasons, those that have focused on the calcaneus, have not done so (Kovarovic 2004, Kovarovic & Andrews 2007, Schellhorn 2009, Schellhorn & Pfretzschner 2015, Barr 2018).

Another explanation for the discrepancy between cervid and bovid studies of the calcaneus, could be that the GMM methods, used in cervid studies so far (Curran 2009, 2012, 2015, this study), more efficiently exclude size differences from the dataset than the linear size corrections often used in bovid studies (e.g. in Kovarovic & Andrews 2007, Barr 2018). It is well established that the use of ratios does not completely eliminate size effects from morphometric variables (Albrecht *et al*. 1993 and references therein). This is only the case when there is a linear relationship between the shape variable and size, an assumption often not met in morphometric datasets (Albrecht *et al*. 1993). Ratios are, however, a commonly used method for size correction in bovid ecomorphological studies (e.g. Degusta & Vrba 2003, Plummer & Bishop 2008). Others (Kovarovic 2004, Kovarovic & Andrews 2007) have not attempted to directly exclude size effects from their dataset, but have used log transformed measurements to satisfy assumptions about normality and homogeneity of variances. It is therefore possible that some residual size differences remain in such datasets. The GPA procedures used in GMM based models, like those developed by Curran (2009, 2012, 2015),

and the ones used in this dissertation, are thought to remove information about size in a much more efficient way from morphometric datasets (Viscosi & Cardini 2011) (see section 5.3) and could potentially explain the limited size effects seen in the currently available cervid studies (Curran 2009, 2012, 2015, this study).

The above explanations may account for the absence of an allometric effect in the cervid calcaneus, but they do perhaps not fully explain the (in some cases more prominent) phylogentic signal found in certain bovid studies (Kovarovic 2004, Kovarovic & Andrews 2007, Barr 2018). As already mentioned, there *was* a phylogenetic effect measured for the calcaneus in the model presented here. The shape components associated with the functional hypotheses (PC1 and PC2) were presumably constrained by phylogeny to some extent. This was expected, because some cervid tribes have an evolutionary history of adaptation to certain habitats (e.g. muntjacs to closed habitats) (Geist 1998).

Degusta and Vrba (2003) argued that phylogenetic effects can be easily excluded from morphometric datasets, by selecting those anatomic features that co-vary with locomotion and habitat. While this is true to some extent, the underlying assumption is that a specific feature is either driven by phylogeny *or* by function. What appeared from the results in this dissertation, is that for most shape traits, this is not possible. Features such as the length of the tuber calcanei are not driven by *either* phylogenetic relatedness *or* functional aspects, but most likely by a combination of both. That being said, the major patterns in the PCA scatterplots in this study were probably still largely dominated by ecologically driven functional differences (see section 6.2.1.3). As such, the critique by Klein and colleagues (2010), that morphological variation in artiodactyls is more driven by phylogenetic relatedness than by function, is unwarranted as far as the calcaneus is concerned. Perhaps the best way to assess the ecological significance of similarities between fossil and extant specimens, is to look at how they behave in a model, *despite* of their taxonomic affinities.

Few ecomorphological works have focused on the intermediate phalanx in artiodactyls. Those that have (Kovarovic 2004, Kovarovic & Andrews 2007, Degusta &Vrba 2005a, 2005b), gave high reclassification rates for this element and agreed that it is a fairly good predictor of habitat, albeit not as good as the proximal phalanx. The effects of phylogeny have not been explicitly tested for the phalanges in any of the mentioned studies (Kovarovic 2004, Kovarovic & Andrews 2007, Degusta &Vrba 2005b), but Kovarovic (2004) acknowledged that phylogeny could explain part of the shape variation. Degusta and Vrba (2005b) trusted that their use of LDA would effectively exclude phylogenetic effects. They assumed that when specimens were grouped by habitat, traits driven by function would be summarized by the first discriminant functions. As has been explained for the calcaneus (see above), this relies on the assumption that a specific morphological trait is driven either by function *or* phylogeny. The results presented in this thesis have, nevertheless, shown that for the intermediate phalanx, those two factors may not be mutually exclusive. Functionally correlated traits such as the overall gracility of the phalanx (summarized by PC1), the depth of the proximal articular surface and the position of the anterior extensor process (PC2) were also driven by phylogenetic relatedness to some extent. The PGLS analysis (see section 6.2.2.4) suggested this was probably even more the case for the intermediate phalanx than for the calcaneus. Nevertheless, the patterns observed in the PCA scatterplots and the fact that many of the functional hypotheses were confirmed, made clear that functional differences were responsible for the majority of the shape variation in this element.

The data in this thesis suggested that the confounding effects of allometry were also limited in the case of the intermediate phalanx. The regression analyses indicated that the functionally correlated traits (as summarized by PC1 and PC2) were to a very small extent driven my allometric differences, but that this probably did not significantly affect the overall shape variation. In other words, larger deer did not necessarily have much more robust intermediate

phalanges or phalanges with deeper proximal articular surfaces than species of small stature. This may be unexpected as some earlier -non ecomorphological- studies on allometry in artiodactyls have noted certain relationships between leg bone size, shape and body weight (Scott 1983, 1985, 1987). Although the specific effects of allometry in the cervid intermediate phalanx are not well studied, a number of workers have considered the problem in bovids. Most of these studies (Kovarovic 2004, Kovarovic & Andrews 2007, Degusta and Vrba 2005b) have made use of linear size corrections to eliminate the effects of body size differences from morphometric variables. While such an approach is probably less efficient in excluding size differences than the GMM methods used here, no significant confounding effects were reported after size corrections (Kovarovic 2004, Kovarovic & Andrews 2007, Degusta and Vrba 2005b). Furthermore, Curran's (2009, 2012, 2015) models of the distal phalanx in cervids did not find allometry to be a strongly confounding factor either. Even though no direct comparison for the cervid intermediate phalanx was available, similar studies at least do not contradict the limited effect of allometry on this element. The fact that the observed morphological differences in these specific traits were not to a large extent driven by size effects, corroborated the idea that the observed morphological variation could be primarily attributed to differences in function

A final confounding factor that has rarely been explored in ecomorphological studies is that of sexual shape dimorphism. A test of the effects of sexual dimorphism in a subsample of specimens indicated that sex played only a small role as a morphological driver in the calcaneus or the intermediate phalanx (see sections 6.2.1.2 and 6.2.2.2). Only limited (non-significant) shape differences were noted between male and female specimens. In spite of the small sample sizes, the data clearly suggested that in the two elements (calcaneus and intermediate phalanx) sexual dimorphism was subordinate to the more prominent interspecific morphological variation.

The effect of sex on limb bone morphology has not been extensively tested in artiodactyl ecomorphological studies (Scott & Barr 2014). Sexual dimorphism is, nevertheless, known in several deer species (e.g. in *Axis axis* and *Elaphurus davidianus*) and is mainly expressed in the presence or absence of antlers and in body size differences (Geist 1998). Some more descriptive studies of bovid morphology have also found differences between males and females in the shape of certain limb bones (e.g. Brugal 1985, Drees 2005, Fernandez & Monchot 2007). It is generally thought that the effects of sexual dimorphism vary between the different elements (Brugal 1985, Drees 2005, Fernandez & Monchot 2007), but that the calcaneus and intermediate phalanx are probably some of the less dimorphic elements (Fernandez & Monchot 2007). An analysis of sexual dimorphism in *Odocoileus virginianus* and *O. hemionus* confirms that this is probably also the case for cervids (Curran 2009).

Looking at this from an ecological perspective, it should, nevertheless, be kept in mind that there is certainly a relationship between sexual dimorphism and ecology (Mysterud 2000). In many deer a sexual segregation exists on the habitat level (Bowyer 2004). Because of differences in body size, social and reproductive strategy, females of certain species tend to have somewhat different requirements than males. This is especially seen in females focusing more on low-fiber/high quality food than males, because of the high nutritional demands associated with gestation and lactation (Clutton Brock *et al.* 1987, Bowyer 2004). Nevertheless, most sexual segregation in cervids manifests itself on a microhabitat level (Clutton Brock *et al.* 1987), while both sexes are still found in the same larger habitats. In other words, as ecological differences between species of different macrohabitats are much more prominent than ecological differences between males and females of the same species, it makes sense that the morphology of the skeletal elements is also primarily affected by larger between-species differences.

Further considerations about fossil applications

It is important to remember that the functional hypotheses on which the predictive models were based relied on the assumption that similar selection pressures (i.e. predator evasion strategy) also drove the morphology of the extinct deer on which the models were applied. In the absence of large predators, especially heavier species will face reduced selection pressure (Scott *et al*. 1991). Although specific body size reconstructions of extinct deer were beyond the scope of this dissertation, earlier work on the cervids from Java (Gruwier *et al.* 2015) has clearly demonstrated that these forms did not fall outside of the normal size range of extant deer in Southeast Asia. With carnivores such as tiger (*Panthera tigris*), leopard (*Panthera pardus*), dhole (*Cuon alpines*), hyena (*Crocuta bathygnatha*) (Storm 2010) and sabertoothed cat (*Homotherium ultimum*) (Volmer *et al*. 2016), there was no lack of large predators in Java during the Pleistocene. As at least some of these carnivore taxa (i.e. tiger, leopard and dhole) are known to focus heavily on large ungulates (Schaller 1967, Nurvianto *et al*. 2016, Rahman *et al.* 2018), it can be assumed that the deer in this region must all have faced considerable predation pressure. Java clearly did not have an impoverished carnivore fauna, as is sometimes seen on the more oceanic islands of the Indo-Pacific (Bouteaux 2005). It could thus be assumed that the Javan fossil deer underwent similar selection pressures, and that their locomotor apparatus was constrained in a similar way as most extant deer.

Another issue that arose from the ecomorphological analyses of the fossils, was the apparent discrepancy between some of the results for the calcaneus and those for the intermediate phalanx. More specifically, in the analyses of the Trinil and *Axis lydekkeri* specimens, the calcaneus was suggestive of a dry, open landscape, while the intermediate phalanx was typical of open or closed environment with wet substrate. This discrepancy might be explained in a number of ways (see below) and it is important to consider the underlying mechanisms that could lie at its basis.

One possible explanation is that the *Axis lydekkeri* specimens from Trinil represent a transitional form that retained certain adaptations from an earlier phase with different environmental conditions. There are in fact indications that the preceding faunal stage in Java was characterized by wetter conditions (Sémah *et al.* 2010, Sémah & Sémah 2012). In this scenario, *Axis lydekkeri* would have retained wet adapted intermediate phalanges from an ancestor adapted to this earlier wet stage, but the calcaneus would have evolved into a dry, open adapted morphotype. This possibility cannot be fully dismissed, but a study by Senter and Moch (2015) has suggested that, generally speaking, phalanges in the mammalian skeleton are more easily reduced to vestigial structures than the elements of the tarsus. This could imply that the calcaneus is morphologically more conservative than the intermediate phalanx and that if *Axis lydekkeri* from Trinil would have retained wet adapted traits from a preceding phase, they would probably be more clearly expressed in the calcaneus.

A second possibility is that the Trinil assemblage contains other, cryptic palaeospecies that were adapted to different habitat types in the surrounding area of the site. In this case the intermediate phalanges would belong to another, more wet adapted species, where the calcanei would belong to more dry adapted species. It was, nevertheless, *a priori* assumed in this thesis that all specimens included in the Trinil dataset belonged to *Axis lydekkeri*. This has also been confirmed by a number of earlier studies that have dealt with the deer from Java (Dubois 1908, Koenigswald 1933, 1934, van den Bergh *et al.* 2001, Gruwier *et al*. 2015). Moreover, given the fairly large dataset for Trinil, it would be expected that if two species were present, a significant portion of the specimens of one element would belong to the same habitat group as the specimens of the other element. As in the results of the ecomorphological analyses almost all the calcanei gave a different ecological signal than the intermediate phalanges, this was probably not the case.

A more likely scenario was that the two elements represented different aspects of the autoecology of *Axis lydekkeri*. In the models developed by Curran (2009, 2012, 2015, 2018), the calcaneus and distal phalanx were pre-assigned to vegetation-type groups (calcaneus) or substrate-type groups (phalanx). Even though in Curran's (2009, 2012, 2015, 2018) work it was predicted that the phalanx would be exclusively driven by substrate type and the calcaneus by vegetation structure, in this dissertation both elements were assigned to combined habitat/locomotor groups that included aspects of both substrate type and vegetation structure. This was done because according to some sources (Leinders 1979) vegetation structure can also affect the morphology of the phalanges to some extent (see section 5.2) and the morphology of the calcaneus may also not be exclusively shaped by vegetation. Despite these assumptions, the results of the ecomorphological analyses confirmed that substrate type was indeed the more important driver of phalanx morphology, while vegetation structure was the principal driver of calcaneus shape.

The apparent discrepancy between ecological signals in different anatomical elements was also noted in a similar study of fossil suids from East Africa (Bishop *et al*. 2006). Instead of interpreting their results as contradictive, they argued that the different elements of the skeleton highlight different aspects of the animals' ecology. In fact, by using these different aspects in concert with each other and with other proxies (e.g. stable isotope analysis), a more detailed picture can be reconstructed (Bishop *et al*. 2006). Accordingly, the results of the Trinil analyses can be interpreted in a similar way. Fossil calcanei similar to those of species of dry, open environment were probably in the first place adapted to an open vegetation structure, irrespective of substrate type. Intermediate phalanges similar to those of species of wet, closed environments were presumably mainly adapted to wet, yielding substrates, irrespective of vegetation structure.

7.3 Palaeoenvironmental reconstructions

Despite a long research history (see section 3.5.2.3), palaeoenvironmental studies of Trinil have lead to conflicting reconstructions (e.g. Van den Bergh *et al*. 2001, Louys 2007, Joordens *et al*. 2009). The results of this study suggested that the cervid species most commonly found there (*Axis lydekkeri*) was associated with a relatively open environment with a wet component (Table 7.1). The Trinil calcanei, shown to primarily signal differences in vegetation structure (see section 6.2.1), were typical of cursorial species found in environments with an open vegetation. The intermediate phalanges conformed to those of cervids adapted to environments with wet, yielding substrates.

Species and provenance	Calcaneus	Intermediate phalanx
Trinil & *Axis lydekkeri*	Typical of (dry) open environments, possibly at high altitude	Typical of (open or closed) environments with wet, yielding substrate
Kedung Brubus unit & *Cervus kendengensis*	Typical of (dry) open environments	Typical of (dry) open or intermediate environments, possibly at high altitude
Sangiran	Typical of (dry or possibly wet) open environments	Combination of a morphotype associated with (open) environments with dry substrate and a morphotype associated with (open or closed) environments with wet substrate

Table 7.1: Summary of the results of the fossil analyses.

These findings generally agree with some more recent interpretations of the Trinil palaeoenvironment as a grassland or open woodland with more densely vegetated river valleys (de Vos *et al.* 1994, Van den Bergh *et al*. 2001, Van der Meulen & Musser 1999, Weinand 2005) (Fig. 7.3). Although certain authors have interpreted Trinil as a closed environment (Selenka *et al*. 1911, Louys 2007), a number of "traditional" palaeontological studies (de Vos *et al.* 1994, Van den Bergh *et al*. 2001, Van der Meulen & Musser 1999, Meijer 2014) have suggested the presence of open woodland, an interpretation confirmed by

isotope studies on artiodactyl bones, that indicated that most Trinil herbivores relied on C4 grasses (Janssen *et al.* 2016) and by an ecomorphological study of bovid astragali (Weinand 2005) (Fig. 7.3). The findings presented in this thesis are in line with a scenario where an open vegetation structure was present around the site, but unfortunately the model did not discriminate well between open woodland and grassland evironments. It is, however, unlikely that Trinil was characterized by a truly open grassland environment, as the (extant) members of the cervid family do not thrive as well in such landscapes as some bovids do (Geist 1998). An open woodland environment, defined here as area with an open canopy of 40% or less closure (Thomas & Packham 2007) is therefore a more likely scenario.

As discussed in section 7.2, there was an apparent discrepancy between the results of the Trinil calcanei and intermediate phalanges. This was explained as a result of different aspects of the animal's ecology being measured. The intermediate phalanges, being a better measure for substrate type than vegetation structure, indicated that Trinil and *Axis lydekkeri* had phalanges adapted for wet, yielding substrates. This suggested that, despite its more open vegetation structure, the Trinil landscape also had a significant wet component.

To what extent this wet signal should be considered a reflection of a localized aspect of the landscape (i.e. the immediate surroundings of the Solo river) or signal a broader phenomenon in the regional environment (i.e. the wider region around Trinil as a wet environment), is not immediately clear from the data. Nevertheless, some reflection on the taphonomy of Trinil and other Quaternary palaeontological sites in equatorial regions, was helpful in this case. In fact, this interpretative problem touches on the wider issue of using animal remains as palaeoenvironmental indicators: to what extent are fossil assemblages representative for the regional mammalian community? Paleontological assemblages are always point collections and it is worth considering at what spatial scale they signal the conditions of the surrounding landscape (Andrews & Hixson 2014).

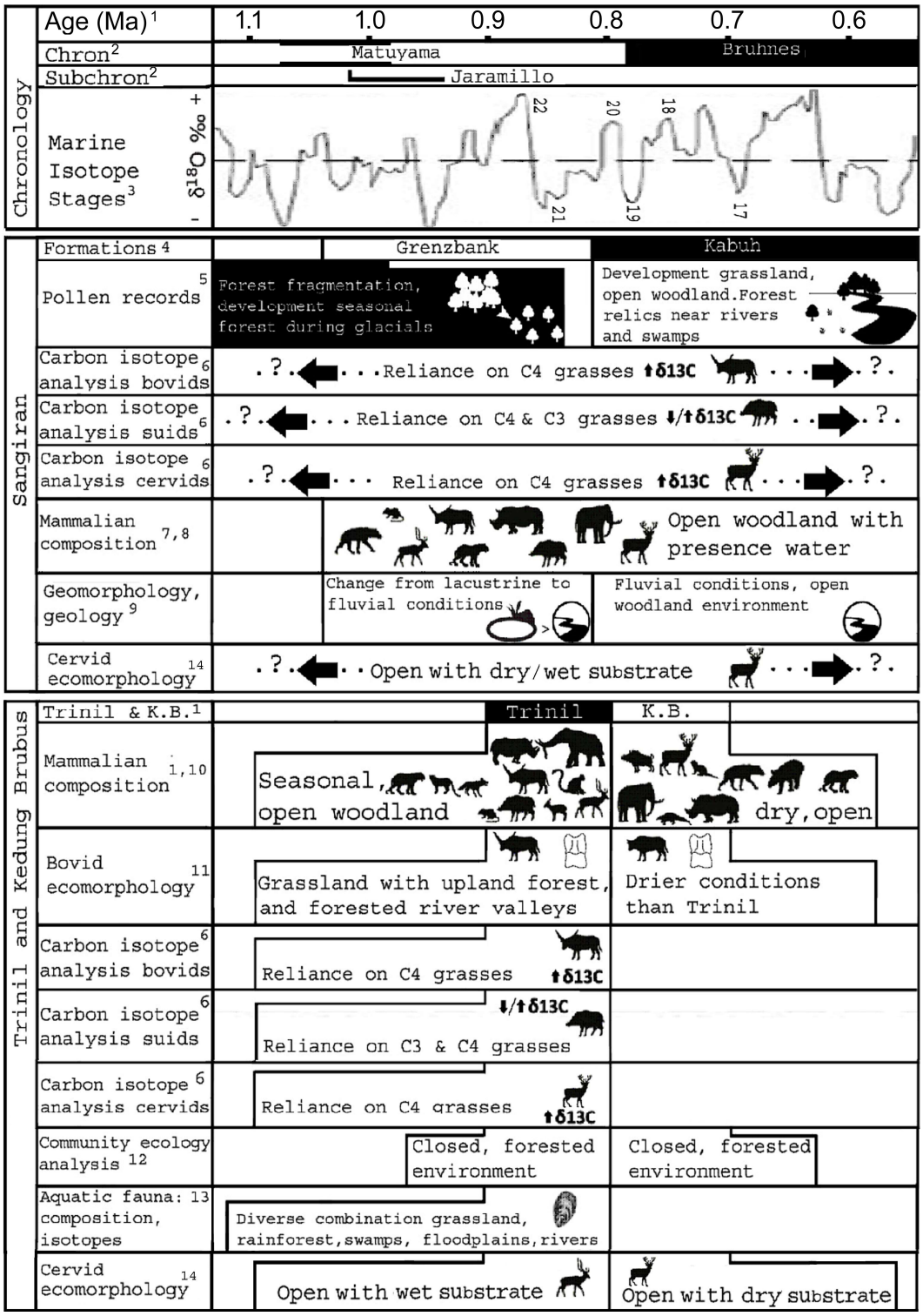


Figure 7.3: Summary of palaeoenvironmental data from Sangiran, Trinil and Kedung Brubus.(1: Van den Bergh et al. 2001, 2: Sagnotti et al. 2014, 3: Head & Gibbard 2005, 4: Indriati & Anton 2008, 5: Sémah 2010, 6: Janssens et al. 2016, 7: Moigne 2004b, 8: Bouteaux 2005, 9: Bettis et al. 2009, 10: Storm 2012, 11: Weinand 2005, 12: Louys 2007, 13: Joordens et al. 2009, 14:this study.(Mammal symbols from Roberts & Amano 2019)

Certain neotaphonomic studies (Andrews *et al.* 1979, Saarinen *et al*. 2010) have tested the relationship between such point collections and the community ecology of the wider area in East Africa. In these cases it was concluded that point collections usually tend to predict the regional mammalian community quite well in e.g. a 50x50 km grid (Saarinen *et al*. 2010).

For Java such experimental studies are non-existent, but some (Storm 2012, Hill *et al.* 2015) have at least considered the problem of representation in the Trinil assemblage. Based on taphonomic arguments (the fluviatile nature of the deposit, the taxonomic composition and lack of evidence for accumulation and selection by animal agents), the Trinil collection was considered a good indicator for the regional palaeocommunity (Storm 2012). Indeed, most palaeoecological studies of Trinil have made use of the vertebrate fossils as a proxy on a regional scale (e.g. de Vos *et al.* 1994, Van den Bergh *et al*. 2001, Van der Meulen & Musser 1999, Weinand 2005). Given that cervid remains (i.e. *Axis lydekkeri*) make up almost a third (NISP) of the vertebrate assemblage (Storm 2012), it is unlikely that they represent an uncommon form that was adapted to localized wet conditions that were perhaps present in the immediate vicinity of the Solo riverbed (Weinand 2005).

The notion that deer fossils signal more regional conditions implies that the wider area around Trinil was characterized by an open, relatively wet environment. This does not necessarily mean that wet conditions were present throughout the year. The wet signal could perhaps also indicate the presence of seasonally flooded plains. This would be in line with the predominance of C4 grasses at Trinil, as indicated by the isotope signatures in some artiodactyl teeth (Janssens *et al.* 2016). In any case, such an interpretation is certainly not unprecedented. Given that the Trinil fossils were excavated from an ancient river terras, geological evidence unsurprisingly indicated wet, fluviatile conditions (Huffman 1997, 1999), but based on a reevaluation of the terrestrial fauna and a number of aquatic biota, Joordens and colleagues (2009) argued for the presence of a regional environment that consisted of

grasslands, floodplains, swamp forest and rivers. An analogy was drawn with the Sundarban swamp forests of Southern India and Bangladesh (Joordens *et al*. 2009). Even though in most other studies (de Vos *et al.* 1994, Van den Bergh *et al*. 2001, Van der Meulen & Musser 1999, Weinand 2005, Janssen *et al*. 2016), including this one, there are indications that the Trinil environment was of a more open nature than that of the Sunderbans, it is plausible that (seasonal) floodplains were a significant part of the Trinil environment. Perhaps a better modern analogy would be Cambodia's northern and eastern plains that are dominated by open deciduous, dipterocarp woodland, alternated by seasonally wet grasslands (Packman *et al*. 2013). Examples of this, now mostly converted habitat type, are still found in reserves such as the Srepok and Phnom Prich wildlife sanctuaries (Cox 2019) (Fig. 7.4).

Figure 7.4: Modern environments found at the Phnom Prich wildlife sactuary in East Cambodia (adapted from Cox 2019) may approach those found at Trinil around c. 0.9 million years ago.

As argued by Joordens *et al*. (2009), the faunal list of Trinil shows a high degree of similarity to that of the Sundarban National Park in India, but both on the specific and generic level the Phnom Prich wildlife sanctuary in Cambodia, is a better match. Taking only mammals above 10 kg into account, Trinil shares 13 taxa (or their closely related extinct counterparts) with the Sundarbans (Joordens *et al*. 2009), but 15 with Phnom Prich (Gray & Phan 2011). Even

though the additional two mammals (a proboscid and *Trachypithecus* sp.) shared with Phnom Prich are not necessarily indicative of a (seasonally) wet, open environment by themselves, they do suggest that the environments found in East Cambodia are at least as similar, if not more comparable, to the Trinil palaeoenvironment.

Axis lydekkeri, the only cervid that was with certainty identified at Trinil, could therefore also be considered a form adapted to (seasonally) wet, open woodland and/or grassland. This was not only confirmed by the isotopic signatures measured on a number of cervid teeth from Trinil (Janssens *et al.* 2016), but also by dental meso-and microwear analyses of Pleistocene *Axis* teeth from elsewhere in Java, that indicated a grass-dominated (mixed) diet (Amano *et al.* 2016). Perhaps its closest ecological equivalent could be *Axis porcinus*, a species currently found in mainland South and Southeast Asia. This cervid is primarily reported from wet grasslands and light woodland and reaches its highest densities in seasonal floodplains (Bhowmik *et al.* 1999). Although *Axis porcinus* is currently under threat, some of its last strongholds are, coincidentally, the remnant wet grasslands and open woodlands of East Cambodia (Maxwell *et al*. 2006). While an assessment of the taxonomic position of *Axis lydekkeri* is beyond the scope of this dissertation, a previous study (Gruwier *et al*. 2015) pointed out that *Axis lydekkeri* was probably also closely related to *Axis porcinus*. In any case, the ecomorphological signature of *Axis lydekkeri* is not the same as that of some other extant members of its genus (e,g, *Axis axis*). This highlights the value of ecomorphological studies, as earlier works have suggested a closer taxonomic and ecological affinity between *Axis lydekkeri* and *Axis axis* from India or the geographically closer *Axis kuhlii* (Dubois 1908, Meijaard and Groves 2004). The latter two species are, nevertheless, adapted to drier environments (Blouch & Atmosoedirdjo 1987) and irrespective of their phylogenetic position, may not be good ecological analogies for *Axis lydekkeri*.

Analyses of the *Cervus kendengensis* remains from the Kedung Brubus unit yielded different results than those of the Trinil cervids (Table 7.1). While the morphology of the calcaneus suggested the presence of relatively open environments, similar to those of Trinil, the phalanx was more indicative of intermediate to dry substrates. Keeping in mind that sample sizes were low, this could imply that the open woodland environments inferred for Trinil persisted during the Kedung Brubus phase, but that the region may have experienced an aridification. Although only limited palaeoecological data is available from other sources for Kedung Brubus (see overview in Figure 7.3), traditional palaeontological analyses of the vertebrate community (de Vos *et al.* 1994, Van den Bergh *et al*. 2001) and an ecomorphological analysis of the bovids (Weinand 2005) have also demonstrated the presence of drier conditions for Kedung Brubus. This fits with the currently accepted biochronological model for the Pleistocene of Java, where the Kedung Brubus phase (ca. 0.7 to 0.8 Ma) is characterized by a new influx of mammal taxa (including *Cervus kendengensis*) from continental Southeast Asia during a glacial maximum (Musser 1982, van den Bergh *et al.* 2001). Although the precise chronology of the Kedung Brubus stage is not well understood, it could potentially coincide with MIS 18 (761-712 Ka) or MIS 20 (814-719 Ka) (Head & Gibbard 2005) (see Fig. 7.3), during which sea levels were low enough to connect Java to the mainland (Voris 2000). The scenario proposed by Louys (2007), where a more forested environment was inferred for Kedung Brubus, was not supported by the data.

Based on its postcranial morphology, *Cervus kendegensis* could thus be considered a species of dry, open woodland and/or grassland. Perhaps its habitat preferences were similar to those of the only member of the genus *Cervus*, still present on Java: *Cervus timorensis* (Geist 1998). Although this species is flexible, it has a preference for dry, open woodland or tropical grassland with some vegetation cover (Medway 1977, Geist 1998). *Cervus timorensis* is particularly common in the savannah environments of far eastern Java, for example found in

the Baluran National Park (Fig. 7.5). This type of environment could perhaps also be considered similar to the palaeoenvironments that were present in the Kedung Brubus area at the beginning of the Middle Pleistocene.

Figure 7.5: Modern environments found at the Baluran National Park in easternmost Java (adapted from Kusuma 2018) may approach those found at Kedung Brubus between 0.7 and 0.8 Ma.

The sample used for the ecomorphological analyses of the Kedung Brubus unit was solely composed of *Cervus kendengensis* specimens, but it should be remembered that *Axis lydekkeri* was not completely replaced during this phase. It merely became much rarer. Where at Trinil, the *Axis lydekkeri* remains still represented approximately 27 % of the total number of identified specimens (NISP), in the Kedung Brubus assemblage this number was reduced to 4 % (van Zelst 2013). In other words, the results of the ecomorphological analyses for Kedung Brubus were driven by the dry, open adapted *Cervus kendengensis*, but the marginal presence of *Axis lydekkeri* during this phase indicated that this species adapted to (seasonally) wet environments was still able to persist to some extent. Perhaps in this case, the more localized wet conditions along the banks of the Solo River acted as a refugium and are reflected in the fossil record. Certain other rare elements in the Kedung Brubus collection, such as the Pleistocene otter *Lutrogale palaeoleptonyx* (Willemsen 1986) support this interpretation.

The results of the ecomorphological analyses of Sangiran suggested that the (unidentified) cervids found there were associated with a wet or dry, but certainly relatively open, environments (Table 7.1). The Sangiran calcanei gave a similar signal as the specimens from Trinil and Kedung Brubus and were typical of species adapted to environments with an open vegetation structure. For the intermediate phalanges a dichotomy between two parts of the sample was noted. The smaller specimens -possibly belonging to the genus *Axis*- were morphologically similar to the more wet adapted cervids from Trinil, while the larger fossils -perhaps belonging to the genus *Cervus*- were morphologically more similar to dry adapted forms such as those from Kedung Brubus.

A problem with the Sangiran collection was that the provenance of the materials is not well known (see Larick *et al.* 2001, Indriati & Anton 2008). Fossils from the Grenzbank and the Kabuh formation were possibly present in the sample, meaning that two distinct phases could be mixed, respectively corresponding to the Trinil H.K. and Kedung Brubus faunal units (see section 5.8.2). This could explain the dichotomy between the *Axis*-sized specimens with a more wet adapted ecomorphological signature and the *Cervus*-sized specimens with a dry adapted ecomorphological signature. The few specimens that certainly belonged to the Grenzbank, were all *Axis*-sized deer with phalanges of a more wet adapted morphotype. This suggested that, at least during the Grenzbank phase, the conditions at Sangiran were similar to those found at Trinil at the end of the Early Pleistocene. The larger *Cervus*-sized specimens would then, presumably, belong to the upper Kabuh formation, corresponding with the drier Kedung Brubus phase. Such an interpretation would be in line with the idea of an aridification in the younger Kabuh formation (Sémah 2010).

Even though it could not be excluded that some of the (dry adapted) *Cervus*-sized specimens were present in the Grenzbank as well, other palaeoecological proxies for Sangiran have been suggestive of a trend towards drier conditions over time (see Figure 7.3). There are

indications in the pollen record for further forest fragmentation. Seasonally wet areas probably became reduced to relics in the immediate proximity of rivers in the Upper Kabuh formation (Sémah 2010). Geomorphological data has also suggested a change from lacustrine to more fluvial conditions during and after the deposition of the Grenzbank (Bettis *et al*. 2009). Palaeozoological studies available for Sangiran have not been specific enough about possible differences between the strata, but confirm the generally open character of the landscape during those periods. The mammalian community was indicative of open woodland with the presence of water (Van der Meulen & Musser 1999, Moigne 2004b, Bouteaux 2005) and stable isotope analyses on cervid, bovid and suid tooth enamel mostly reflected a reliance on C4 grasses, similar to Trinil (Janssens *et al*. 2016).

Although the chronological correlation of the formations at Sangiran with the Trinil (H.K.) and Kedung Brubus faunal units is a point of discussion (Indriati & Anton 2008), the results presented in this thesis suggest that, generally speaking, the conditions in East Java at the end of the Early Pleistocene and the beginning of the Middle Pleistocene were continually of an open nature. Throughout the studied period, the landscape was dominated by open woodland (and/or grassland) with at least some tree cover. At the end of the Early Pleistocene the landscape in the region was probably also characterized by the presence of seasonally wet floodplains. During glacial maxima, climatic changes occurred that led to aridifcation, further forest fragmentation and the possible disappearance of these (seasonally) wet environments. Nevertheless, even in these drier phases, refugia with wetter conditions must have persisted in the immediate vicinity of large streams. Truly closed forest conditions, such as those currently found in far western Java and on other Sundanese islands such as Borneo (Nooteboom 1992), were apparently not present in East Java during the late Early and early Middle Pleistocene. Presumably such conditions did not appear in the region before the advent of the Punung faunal stage (60 to 120 Ka) (Badoux 1959, van den Bergh *et al.* 2001).

7.4 *Homo erectus* palaeoecology and significance to dispersal theories

Although the ecomorphological models did not differentiate well between open woodland and grassland, the results of the analyses were all indicative of relatively open conditions - probably open woodland- in the surroundings of the studied *Homo erectus* localities. As has been explained in section 7.3, this was largely in line with data from a number of other proxies for these sites (e.g. Indriati & Anton 2008, Sémah 2010, Janssens *et al.* 2016, Moigne 2004b, Bouteaux 2005, Weinand 2005). Palaeoecological data from other *Homo erectus* sites are sparse for Java, but the limited data from Ngandong were also indicative of open woodland environment (de Vos *et al.* 1994, van den Bergh *et al.* 2001, Huffman *et al*. 2010).

Generally speaking the results of the ecomorphological analyses, especially in concert with other palaeoenvironmental data (e.g. Indriati & Anton 2008, Sémah 2010, Janssens *et al.* 2016, Moigne 2004b, Bouteaux 2005, Weinand 2005), confirmed the idea that *Homo erectus* was primarily associated with open environments.This interpretation fitted to a certain extent with the idea that the expansion of open environments in Asia and Africa during the Plio-Pleistocene was an important driver of early hominin dispersal (Bonnefille 1984, Prentice & Denton 1988, Demenocal 1995, Vrba 1996, Dennell & Roebroeks 2005, Dennell 2010). In this scenario, dry, open landscapes, became especially prominent around 1.8 Ma, coinciding with the appearance and range expansion of *Homo erectus* across large parts of the Old World (Dennell & Roebroeks 2005, Dennell 2010). In Pleistocene Southeast Asia this would have taken shape in the form of a savannah corridor that stretched from the Asian mainland, over the exposed Sunda shelf, to Java (Heaney 1991, Bird *et al.* 2005). Such a continuous tract of more open habitat would have allowed *Homo erectus*, alongside a range of other mammals, to colonize Sundaland (Bird *et al.* 2005).

It should, nevertheless, be said that the open environments, supposed to drive early hominin dispersal, are often interpreted as dry, savannah-like grasslands, that appeared in a context of wider aridification in the Northern Hemisphere (Bonnefille 1984, Prentice & Denton 1988, Demenocal 1995, Vrba 1996, Dennell & Roebroeks 2005, Dennell 2010). The environments reconstructed for the Javan sites, on the other hand, seem to be characterized by a somewhat more closed vegetation structure (open woodland) than what is suggested in the Savannahstan model (Dennell & Roebroeks 2005, Dennell 2010). While the evidence does not contradict an extrinsic explanation where climate change and the appearance of more open environments in Africa and Asia played a role in *Homo erectus* dispersal, it is likely that the ecological reality on a regional level was probably one of considerable variation. It should be remembered that global climatic changes, as for example evidenced in marine isotope records (e.g. Prentice & Denton 1988) are regionally expressed in different ways under the influence of a complex combination of forcing mechanisms (e.g. the position of the ITCZ and ocean surface temperatures), that are –especially for the tropics- not well understood (Burnett *et al.* 2011). Although a global arridification in the Late Pliocene and Early Pleistocene likely resulted in the development of corridors of more open vegetation across the *Homo erectus* range, this idea somewhat obscures the notion that within the context of those climatic conditions, there was still room for a range of different (open) habitats, many of which were probably suitable for *Homo erectus*. In island Southeast Asia such suitable habitat was probably present in the form of an open woodland setting. In other regions, however, such as North Africa, *Homo erectus* seems to have also thrived in habitats with a more limited tree cover (Geraards 1980, 1993, 1994). This testifies to a certain ecological flexibility in this species.

A further argument for such a flexibility lies in the wet component inferred for Trinil (this study and Joordens *et al*. 2009). This is an important issue, considering that some other *Homo erectus* sequences from Java, besides Trinil, have also indicated the presence of wet

conditions. For the Pucangan formation at Sangiran, marshy and lacustrine conditions have been suggested (Aimi & Aziz 1985, van den Bergh et al. 2001, Bouteaux 2005) and at Mojokerto a mangrove or swamp environment was possibly present (Huffman & Zaim 2003). Despite the fact that a wet component in the landscape does not contradict the presence of relatively open environments, such conditions are more difficult to reconcile with the often emphasized Plio-Pleistocene aridification in the hominin dispersal narrative (Vrba 1996, Dennell & Roebroeks 2005, Dennell 2010). This potential incompatibility is illustrated by the position of Dennell (2010), who in fact recognized the presence of swamp-like conditions in the Pucangan formation at Sangiran, but argued that the hominin remains found there were probably washed down from a drier region upstream.

It is certainly possible that some of the Sangiran hominins were not *in situ*, but it is unlikely that this was also the case for the *Homo erectus* remains from Trinil. In fact, there are no indications at Trinil that the processes of accumulation, sedimentation and preservation were different for the hominin fossils than for the majority of the other faunal remains (Hill *et al.* 2015). Furthermore, it should be remembered that the wet signal measured for the Trinil cervids does probably not merely reflect localized wet conditions in the immediate vicinity of the Solo river (see section 7.3). It should therefore be considered plausible that, despite an apparent preference for open environments, *Homo erectus* was not only capable of coping with a range of open conditions, but also more marshy conditions, seasonally wet habitats or floodplains. Indeed, there is even some evidence for the active exploitation of such environments in the form of a number of aquatic mollusk remains from Trinil. As all the shells found there were of a uniformous, large size and because the identified specimens all belonged to taxa that are currently still known as edible, the shells were probably consumed after being collected from shallow waters (Joordens *et al.* 2009).

Looking at *Homo erectus* from a diachronic perspective, it seems that this species was able to survive significant environmental changes that occurred along the glacial-interglacial cycles of the Early and Middle Pleistocene. Although Trinil, Kedung Brubus and the different formations at Sangiran are difficult to correlate with each other and with specific stages in climatic history, the potential aridification noted from the Trinil to the Kedung Brubus phases, also testifies to a certain adaptive flexibility in *Homo erectus*.

This inevitably leads to the question; which specific aspects of the environments of the Plio-Pleistocene constrained *Homo erectus* dispersal and success? From the apparent omnipresence of open landscapes at the hominin sites in Java, the impression emerges that vegetation structure was probably an important criterion. A plausible explanation for this could be that *Homo erectus* focused its hunting strategy on large mammals of open environments. It is sometimes argued that hominins, around this time, underwent a shift from occupying a primarily omnivorous niche to becoming top predators (Turner 1999, Carotenuto *et al.* 2016). Perhaps *Homo erectus'* adaptive strategy was based on following such animals along the large tracts of savannah-like open environment that ranged from East Africa to Southeast Asia (Shipman & Walker 1989, Cachel & Harris 1998, O'Regan *et al.* 2011, Carotenuto *et al.* 2016, Roberts & Amano 2019). Whether or not these open habitats regionally consisted of arid grasslands, open woodlands or on occasion of floodplains or open swamps may not have been decisive, as long as sufficient and accessible protein resources were available. The presence of a minimum of tree or shrub cover would, however, have been advantageous, as this would have provided cover for concealement or ambush hunting (Finlayson 2011). In closed, forested environments, where such resources are scarce, unevenly distributed and more difficult to access (Bailey *et al*. 1989), *Homo erectus* probably met the limits of its adaptive flexibility.

It is interesting to note that in almost all *Homo erectus* localities in Southeast Asia, the dominant mammals are *Stegodon*, large bovids and suids, forms generally adapted to open environments (van den Bergh *et al*. 2001, Roberts & Amano 2019). This pattern not only emerges from the currently known *Homo erectus* sites in the region, but also from other localities with evidence for the presence of pre-modern hominins, such as Liang Bua, where *Homo floresiensis* was found (Brown *et al.* 2004) and some recently studied sites like Kalinga in the Philippines (Ingicco *et al.* 2018) and Talepu on Sulawesi (van den Bergh *et al*. 2016). So despite the fact that early hominins may have crossed the Wallace line and occupied more oceanic islands with accessibility to other resources (e.g. marine shells or birds), the earlier members of our genus seem to have largely retained their adaptive strategy focused on large mammals of open environments (Roberts & Amano 2019). Evidence for human presence in closed, forested habitats in Southeast Asia does not appear before the Late Pleistocene. At sites such as Niah cave in Borneo (Barker *et al.* 2007, 2009*)* and Braholo (Amano *et al*. 2015) and Punung (Badoux 1959) in Java, hominins clearly subsisted on forest resources, but these sites have all been associated with *Homo sapiens*.

Looking at *Homo erectus* palaeoecology on a continental scale a similar picture emerges (Table 7.2). Most, if not all, of the principal sites are characterized by relatively open environments, but with significant regional differences. In East Africa, where *Homo erectus* probably originated, most sites -including Olduvai, Koobi Fora and Melka Kunture- are characterized by what seems to be a relatively dry, open woodland savannah (Bonnefille 1972, 1984, Gentry 1978, Pichon 1979, Sabatier 1982, Shipman & Harris 1988, Bobe *et al.* 2007, Behrensmeyer *et al.* 2016). In terms of vegetation structure, it could therefore be said that the conditions *Homo erectus* encountered in Java, where not that different from those in which it presumably evolved in East Africa.

Site	Age	Palaeoenvironment
Tomas Quarries, Morocco	0.4 Ma [1,2]	Dry, open environment [25,26,27]
Ternifine, Algeria	0.7 Ma [3]	Dry, open environment with seasonal lake or swamp [3,28]
Sidi Abderrahman,	Middle Pleistocene[4]	Dry, open environment [29,28]
Olduvai (Bed II), Tanzania	1.6-0.6 Ma [5]	Dry, open bush with savannah or wooded grassland [30,31,32,33]
East Turkana (Koobi Fora), Kenya	1.8-1.9 Ma [6,7]	Dry, open, wooded savannah with lake margins and riverine environments [34,35,36,37,38]
West Turkana (Nariokotome), Kenya	1.5-1.6 Ma [8]	Open, seasonally arid grasslands [34]
Olorgesaillie, Kenya	0.9 Ma [9]	Open, wetland conditions [39,40]
Melka Kunture, Ethiopia	0.7-1.7 Ma [10]	Dry, open, savannah-like conditions, woodland savannah with presence water [41,42,43,28,44]
Bodo, Ethiopia	Middle Pleistocene [11,12]	Open grassland, with presence of water [45,46,47]
Swartkrans, South Africa	Early Pleistocene [13]	Open grassland, with woodland on the riverside [48,49]
Dmanisi, Georgia	1.78-1.85 Ma [14,68]	Dry forest steppe with forested mountains nearby [50,51,52,53]
Kocabas, Turkey	Early to Middle Pleistocene [15]	Swamp-like conditions, surrounded by dry limestone hills [54]
Zhoukoudian, China	0.4-0.6 Ma [16,17,69]	Dry forest steppe, with alternating stages with increased forest cover [55,56,16,57,58]
Xujiayao, China	0.26-0.37 Ma [18]	Temperate to cold lacustrine conditions, forest steppe? [59,60,61]
Gongwangling, China	0.75-0.8/1.63 Ma? [19,70]	Alternating cold and warm, but dry conditions [16]
Chengjiawo, China	0.65 Ma [20]	Steppe, probably forest steppe [62,16]
Trinil, Java	0.9 Ma [21]	Open woodland with (seasonally) wet component [63,21,64,65,this study]
Sangiran, Java	1.6-0.7 Ma [22,23,24]	Open, initially wetland conditions, later more arid but with wet component [21,65,66,67, this study]
Kedung Brubus, Java	0.7-0.8 Ma [21]	Dry, open woodland[63,21, this study]
Ngandong, Java	108-117 Ka [71]	Open woodland [63,21]
Mojokerto, Java	1.8 Ma? [22]	Mangrove or swamp environment [68]

Table 7.2: Summary of palaeoenvironmental reconstructions for the principal Homo erectus sites in Africa and Asia (1: Sausse 1975, 2: Hublin 1985, 3: Geraards et al. 1986, 4: Arambourg &Biberson 1956, 5: Rightmire 1979, 6: Leakey & Walker 1976, 7: Day 1971, 8: Brown et al. 1985, 9: Potts et al. 2004, 10: Raynal et al. 2004, 11: Asfaw 1983, 12: Asfaw et al. 2002, 13: Curnoe et al 2001, 14: Gabunia et al. 2002b, 15: Vialet et al. 2012, 16: Zhu & Zhou 1994, 17: Zhou et al. 2000, 18: Ao et al. 2017, 19: An et al. 1990, 20: Liu 1985a, 21: van den Bergh et al. 2001, 22: Swisher et al. 1994, 23: Sémah et al. 2010, 24: Indriati & Anton 2008, 25: Geraards 1980, 26: Geraards 1993, 27: Geraards 1994, 28: Bocherens et al. 1996, 29: Raynal et al. 2002, 30: Gentry 1978, 31: Shipman & Harris 1988, 32: Bonnefille 1984, 33: Ashley et al. 2010b, 34: Bobe et al. 2007, 35: Behrensmeyer et al. 2016, 36: Kappelman et al. 1997, 37: Plummer et al. 2015, 38: Bonnefille 1976, 39: Behrensmeyer et al. 2002, 40: Kübler et al. 2015, 41: Bonnefille 1972, 42: Pichon 1979, 43: Sabatier 1982, 44: Geraards et al. 2004, 45: Kalb et al. 1980, 46: Barboni et al. 1999, 47: Ambrose et al. 2016, 48: Vrba 1975, 49: Avery 1995, 50: Gabunia et al. 2000a, 51: Gabunia et al. 2001, 52: Messager et al. 2010, 53: Blain et al. 2014, 54: Lebatard et al. 2014, 55: Li & Ji 1981, 56: Liu 1985b, 57: Jin et al. 1999, 58: Gaboardi et al. 2005, 59: Chia et al. 1979, 60: Pei et al. 2009, 61: Wu & Trinkaus 2014, 62: Wu et al. 1989, 63: de Vos et al. 1994, 64: Van der Meulen & Musser 1999, 65: Joordens et al. 2009, 66: Moigne et al.2004b, 67: Bouteaux 2005, 68: Huffman & Zaim 2003), 68: Ferring et al. 2011, 69: Shen et al. 1996, 70: Zhu et al. 2015, 71: Rizal et al. 2020.

Although recent reanalyses have added nuance to some of the drier reconstructions in East Africa (Kovarovic *et al.* 2013, Dominguez-Rodrigo *et al*. 2010), some sites in this region (Nariokotome, Bodo), but especially in North Africa (Sidi Abderrahman, Ternifine, Tomas Quarries), give evidence that *Homo erectus* was also present in drier, open grassland conditions (Geraards 1980, 1986, 1993, 1994, Kalb *et al.* 1980, Bocherens *et al.* 1996, Barboni *et al*. 1999, Raynal *et al.* 2002, Bobe *et al.* 2007). Even though it should be taken into account that these sites are considerably younger than some of the early East African sites, it demonstrates that *Homo erectus*, at some point successfully adapted to different conditions than those in which it originally evolved.

The same can be said for certain sites such as Olorgesaillie and Kocabas that were probably characterized by swamp-like environments (Behrensmeyer *et al*. 2002, Lebatard *et al*. 2014, Kübler *et al*. 2015). Even more so than Trinil, they show that, across its range, *Homo erectus* was equally capable of coping with (open) wetland conditions as with drier environments. While true wetland conditions are unlikely to have been an absolute requirement for *Homo erectus*, the presence of at least some standing water probably was. This idea is supported by the notion that for the majority of the *Homo erectus* sites (see Table 7.2) there are indications for some kind water reservoir in the vicinity. This is even the case for the North African sites, that despite their aridity probably also boasted seasonal lakes or swamps (Geraards 1980, 1986, 1993, 1994, Raynal *et al.* 2002). This could suggest that access to water was also a constraining factor in early hominin distribution.

As the Pleistocene hominin record of continental Asia remains largely unknown, it is difficult to make generalizations about *Homo erectus* palaeoecology in this region. Based on the few sites, that are far apart and not all studied in the same detail (Table 7.2), it seems that *Homo erectus* was mainly found in relatively open forest steppe conditions (Chia *et al.* 1979, Li & Ji 1981, Liu 1985b, Wu *et al.* 1989, Zhu & Zhou 1994, Jin *et al.* 1999, Gabunia *et al.* 2000a,

2001, Pei *et al.* 2009, Messager *et al*. 2010, Blain *et al.* 2014). In terms of vegetation structure this type of environment is not unlike the open, wooded savannah environments of the Early-Middle Pleistocene of East Africa and Java. This observation lends further support to the Savannahstan model that stresses the importance of similar, open environments for the early dispersal of hominins in Asia (Dennell & Roebroeks 2005, Dennell 2010). On the other hand, as was the case in Africa, drier and more open (steppe) environments seem to have also been occupied in mainland Asia (Zhu & Zhou 1994). Interestingly, some of these sites with drier stages (e.g. Gongwangling, Xujiayao an Zhoukoudian) not only suggest changes in aridity over time, but also in temperature (Kurten & Vasari 1960, Chia *et al.* 1979, Li & Ji 1981, Wu *et al.* 1989, Zhu & Zhou 1994, Wu & Trinkaus 2014, Li *et al.* 2016). Apparently even the colder stages in these sequences did not form a major obstacle for *Homo erectus*. Rather than limiting its success as a species, it is more likely that *Homo erectus* was capable of making optimal use of these environments.

It thus seems that, within the constraints of relatively open environments, *Homo erectus* was a flexible species with a preference for open, wooded savannah-like environments within the proximity of water or wetlands. This type of environment, becoming more prominent over the course of the Early and Middle Pleistocene, probably at least facilitated its dispersal. Whether this means that intrinsic changes in the hominin lineage only played a minor role in its success and dispersal, cannot be said based on the current evidence. Given its success in a range of different (open) environments, it is plausible that *Homo erectus* was well suited to cope with the increasing climatic oscillations of the Plio-Pleistocene, as proposed in Potts' (1998) variability selection hypothesis. It is, nevertheless, unclear whether in this aspect it differed significantly from its predecessors. What seems more evident, is that the degree of adaptive flexibility currently seen in modern humans, was probably something that appeared at a later stage in human evolution. The engagement of *Homo sapiens* with a wide range of

environments, including closed tropical rainforest and arctic conditions, is not only testified by studies of contemporary hunter-gatherer societies (Kelly 2013, Cosgrove 2015), but also by archaeological evidence from across Southeast Asia (e.g. Badoux 1959, Barker *et al.* 2007, Amano *et al*. 2015, 2016).

7.5 Further considerations about the statistical analyses

This study primarily made use of between-groups PCA to explore morphological variation in the datasets (see section 5.5). To quantify the significance of the between-group separations in the clusters generated by the PCA's, Kruskal-Wallis tests were conducted on the PC-scores, followed by post-hoc pairwise comparisons to explore which pairs differed significantly. The Kruskal-Wallis test is a rank-based test and functions as a statistical procedure to test the null hypothesis that several univariate samples are taken from populations with equal medians (Hammer 1999, Corder & Foreman 2009). As in this dissertation, it was also important to assess *which* groups differed from other groups, post-hoc testing was conducted to analyse specific pairs for significant differences (Goodpaster & Kennedy 2011). Although there is currently no standard metric to quantify cluster separation in PCA (Goodpaster & Kennedy 2011), there are also other statistical approaches (see below) that could have been employed to assess the significance of the separations generated by the PCA's. Some of these alternative methods could potentially improve the results of this dissertation.

The approach used in this thesis followed established procedures from the literature to determine significance of groups in the PCA scores (Lynch *et al.* 1999, Harvati 2003, 2004, Nicholson & Harvati 2006, Yao *et al*. 2013). Due to the nature of the geometric morphometric data a non-parametric test (the Kruskal-Wallis test) was required to assess between-group differences (Yao *et al.* 2013). The reason for this was that, despite the fact that individual principal components are orthogonal and can be treated as mathematically independent

variables (Polly & Motz 2016), the GMM data on which the linear recombinations of the PCA are based, tend to violate statistical assumptions such as normal distribution (Cardini *et al.* 2015). For the pairwise comparisons the commonly used Mann-Whitney pairwise test was chosen. Although other post-hoc tests, such as Dunn's test (Dunn 1964) or the Conover-Iman test (Conover & Iman 1979), can be used in conjunction with the Kruskal-Wallis test, the Mann-Whitney pairwise test was preferred as it performs well on small datasets with unequal sample sizes (Mann & Whitney 1947, Nachar 2008).

However, in pairwise comparisons, where statistical tests are repeated multiple times, it is often advisable to re-calculate probabilities to control the Type I error rate (Conover & Iman 1979). There are several procedures available for multiple comparison correction, including Holm's method (Holm 1979), the Benjamini-Hochburg procedure (Benjamini & Hochburg 1995) and the commonly used Bonferroni correction (Dunn 1961, 1964). While all these methods provide more or less stringent control of Type I errors, they have the disadvantage that the likelihood of Type II errors increases and important between-group differences can be missed (Perneger 1998, Gelman *et al.* 2012).

In this dissertation the uncorrected *p*-values of the Mann-Whitney pairwise comparisons were reported. Even though the Kruskal-Wallis Mann-Whitney procedure is thought to provide a better balance between type I and type II errors than some other methods, such as Dunn's test (Conover & Iman 1979), it is possible that the lack of multiple corrections has led to a number of false positives. In the light of continued research, it may therefore be useful to provide additional corrected *p*-values for the analyses of the calcaneus and intermediate phalanx. Most correction procedures (e.g. Holm's method) are, however, more appropriate for parametric tests, so in the context of the non-parametric analyses conducted in this thesis the use of Bonferroni correction would be most advisable (Shiratsuchi *et al.* 2006). It should, nevertheless, be mentioned that Bonferroni corrected values should be interpreted with some

caution as well, as this correction procedure is conservative and tends to inflate the number of Type II errors (Armstrong 2014).

The implications of not using multiple correction in this study can only be fully appreciated with additional tests on the datasets. Nevertheless, as the Bonferroni correction is a relatively simple procedure that adjusts the α-value to the number of comparisons (Perneger 1998), it follows that those significant between-group differences that show the highest uncorrected *p*-values will be the most likely candidates to appear as non-significant after correction. This was confirmed by unreported preliminary tests on the datasets with the extant calcanei and phalanges. Bonferroni corrected Mann-Whitney pairwise comparisons conducted on the data altered the initial results, but showed that, for both elements, it was often the type 2 (intermediate species) and type 4 group (mountain species) that gave non-significant differences after correction. This implies that mainly those groups that were already shown to have a high degree of visual overlap in the PCA scatterplots, could also not be reliably separated in the pairwise comparisons following the Kruskal-Wallis test. Consequently, between-group differences that were supported by the latter test, but not by visual assessment of the scatterplots, should be cautiously interpreted. As the interpretation of the trends observed in the analyses in this thesis already relied heavily on the visual interpretation of the scatterplots, it is not unreasonable to assume that the ultimate categorization of the fossil groups would not be altered to a large extent after additional corrections. This was confirmed by an unreported preliminary reanalysis of the Trinil calcanei dataset. The uncorrected pairwise comparisons following the Kruskal-Wallis test on PC1 of the Trinil calcanei indicated non-significant differences between the fossils and the type 4 group (p=0.5832). After the Bonferroni corrections the pairwise comparisons gave non-significant differences between the fossils and the type 4 group (p=1) and the type 1 groups (p=0.1204). This is an interesting observation, as the Trinil calcanei were ultimately interpreted as similar to the type

1 *and* type 4 groups, based on visual assessment of their position in the PCA scatterplots. Further reanalyses of the data will have to confirm if this will also hold for other datasets.

Despite the fact that Bonferroni corrections could provide extra nuance to the interpretation of the results of the univariate tests, it should be mentioned that other approaches are possible for testing between group significance in PCA besides the Kruskal-Wallis Mann-Whitney procedure. In this context, improvement could be sought in the further use of multivariate methods, which was already explored to an extent with the NPMANOVA. Even though these methods will not assess between-group significance of individual component scores, for theoretical reasons they may be more reliable as an indicator for the significance of group separations in a PCA. This is because, even though individual components can technically be treated as independent variables, the underlying biological shapes on which they are based are multivariate in nature (Polly & Motz 2016). A multivariate analysis may therefore pick up differences not registered on a single axis. An alternative method that has been applied, besides the NPMANOVA, is the use of a two-sample Hotelling's T^2 test on the distance between group centroids, where an F-test is conducted to determine if cluster separations are significant (Goodpaster & Kennedy 2011). But for GMM-based datasets such an approach is not ideal, as this test assumes normal distribution. Moreover, the challenge remains that multivariate approaches are only of limited help with the interpretation of individual scatterplots.

One simple solution that avoids conducting additional univariate tests on the PC-scores, but helps with the visual interpretation of the clusters in the PCA scatterplots, is to provide simplified one-dimensional plots of Euclidean distances between cluster centroids (Goodpaster & Kennedy 2011). In this method plots are generated that visualize the distance between group centroids compared to the distances between individual points within a cluster (Goodpaster & Kennedy 2011). To illustrate, an example based on a small subset of extant

calcanei is provided in Figure 7.6. A list with used species and specimens is provided on the right side of the graph.

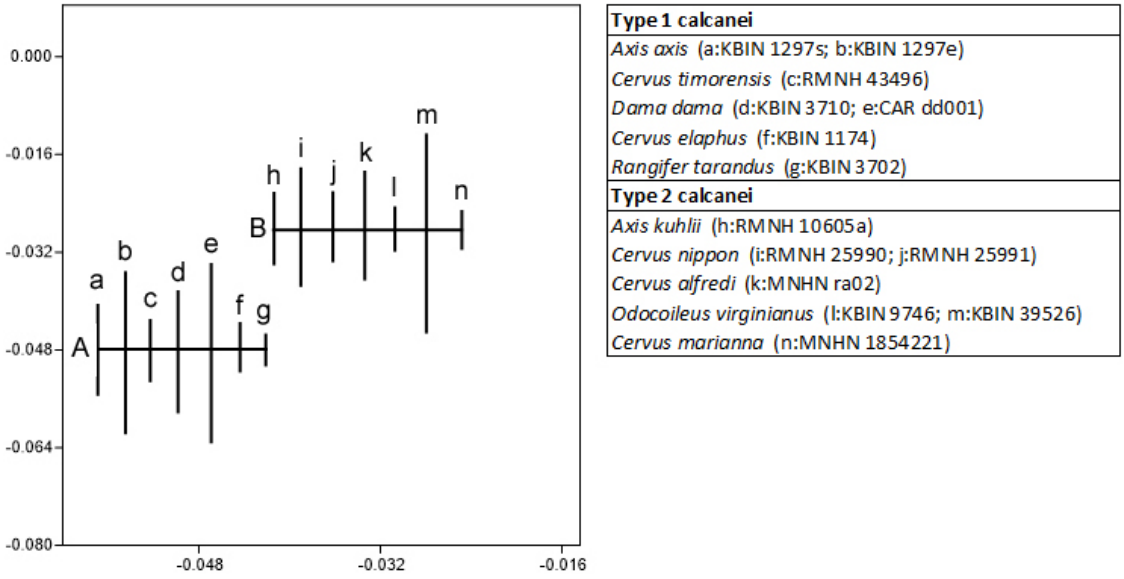


Figure 7.6: One-dimensional plot of Euclidean distances between cluster centroids of a PCA scatterplot of a sample of seven type 1 calcanei (a,b,c,d,e,f,g) and seven type 2 calcanei (h,i,j,k,l,m,n). The centroid of each group is represented by a horizontal line (A and B), where the distance between A and B is the Euclidean distance between the two group centroids. The vertical lines (a to g and h to n) visualize the distance from each datapoint to its group centroid.

In summary it can be said that, although there were reasons that justified the use of the current protocol (i.e. the need to quantify separations between each group in individual scatterplots using non-parametric tests), there are possibilities to improve the results in this thesis. Future improvements include providing Bonferroni-corrected *p*-values in addition to the uncorrected *p*-values. That being said, the results of the Kruskal-Wallis test and following pairwise comparisons should be cautiously interpreted, and only in conjunction with visual assessment of the PCA scatterplots and the results of the NPMANOVA. One-dimensional plotting of the Euclidean distances between group centroids could be a useful additional way to help with the visual interpretation of group differences in the scatterplots.

8. Conclusion

This thesis had two primary objectives. A first goal was to construct ecomorphological models for the cervid intermediate phalanx and calcaneus that can be used to make predictions about the nature of ancient environments. The second objective was to apply these methods on a number of Javan Pleistocene sites to contribute to a more detailed palaeoenvironmental framework for this region and to provide context to the behaviour and early dispersal of *Homo erectus*. Emphasis was placed on assessing the ecological flexibility of this hominin species by examining the nature and significance of environmental differences between sites. Specifically, by comparing materials from the Kedung Brubus faunal unit with those of the Trinil (H.K.) faunal unit and from Sangiran, the aim was to assess whether an environmental and/or climatic shift could be discerned in the fossil record. It was hoped that the results of these analyses would be informative about the extent to which *Homo erectus* was associated with a specific type of environment. As such, this study was also conceived as a test whether the conditions were met in Java for a scenario where early hominin dispersal was largely driven by extrinsic factors. Addressing these research questions did not only lead to new and valuable insights pertaining cervid ecomorphology, but also successfully contributed to our understanding of *Homo erectus* behaviour and palaeoecology in Java and further afield.

Building on previous research in artiodactyl ecomorphology, it has been demonstrated that the morphology of the cervid calcaneus and intermediate phalanx can be used to predict the habitat preferences of (extinct) taxa of unknown ecological affinity. The shape of the two studied elements varied along a continuum from open habitats with dry, firm substrate to closed habitats with wet, yielding substrate. The shape of the calcaneus was found to be primarily a good predictor of vegetation structure, while the intermediate phalanx was demonstrated to be mainly indicative of substrate type. As such, the two elements were

confirmed to be good indicators of different ecological aspects in the regional environment. The ecomorphological methods presented here, in other words, provide a valuable new proxy for palaeoenvironmental reconstruction of Pleistocene sites. The possibilities for applying these new methods are, moreover, not limited to palaeoanthropological sites in Southeast Asia. As the models were broadly conceived and included a large and taxonomically balanced sample of extant cervids from across the globe, they could theoretically be applied on any site with sufficient deer fossils.

It was further demonstrated that the use of 3D GMM forms an improvement over the linear morphometric analyses usually used in similar studies. In addition to allowing for more subtle morphological differences to be analyzed, the deformation grids reconstructed from the morphometric data, allowed for a much needed visualization of the quantified shape differences. This proved to be especially helpful for interpreting the underlying causes and functional significance of morphological variation. The introduction of a functional framework, where shape differences can be explicitly tested against predetermined functional hypotheses, represents a novel –but enhanced- approach in artiodactyl ecomorphology. By assessing morphological differences against this framework, in concert with other statistical tests (i.e. PGLS, linear regressions), it was shown that the confounding effects of a number of factors (including size, sexual dimorphism, anterior/posterior position and phylogeny) did not interfere to a large extent with the predominantly functional signal measured in the datasets.

The application of the ecomorphological methods on the hominin sites from Java added significantly to our current knowledge of the Pleistocene environments in this region. The analyses of Trinil and the cervid species most commonly found there (*Axis lydekkeri*), indicated the presence of an open environment -probably an open woodland environment- with a (seasonally) wet character. This interpretation corroborated earlier reconstructions of the Trinil palaeoenvironment (de Vos *et al.* 1994, Van den Bergh *et al*. 2001, Joordens *et al*.

2009), but rejected interpretations of Trinil as a closed, forested environment (Selenka *et al.* 1911, Louys 2007). *Axis lydekkeri* itself was argued to have been ecologically analogous to the extant *Axis porcinus*, a species of wet grasslands and open woodlands, and not to certain other members of the genus (*Axis axis* and *Axis kuhlii*) that have in the past been considered closer equivalents (Dubois 1908, Meijaard and Groves 2004). This notion underlined the value of ecomorphological studies in identifying the habitat preferences of extinct species.

Kedung Brubus and the species most commonly found there (*Cervus kendengensis*), were shown to be associated with open conditions that were more arid than those reconstructed for Trinil. This was in line with a number of earlier studies of the Kedung Brubus palaeoenvironment (de Vos *et al.* 1994, Van den Bergh *et al*. 2001, Weinand 2005), but challenged the idea that it was characterized by a closed, forested environment (Louys 2007). The (seasonally) wet component found in the older Trinil stage largely disappeared during the younger Kedung Brubus stage. *Cervus kendengensis* was interpreted as ecologically analogous to *Cervus timorensis*, a species currently still present on Java. This new arrival from the Asian mainland was most likely able to colonize Java as part of a larger influx of new species during a glacial maximum when Sundaland was connected to continental Southeast Asia.

For Sangiran reconstructions also confirmed the presence of open conditions, as has been suggested in the literature (Moigne 2004b, Bouteaux 2005, Sémah 2010, Janssens *et al*. 2016). The sample consisted of a combination of fossil specimens indicating dry substrate as well as others indicating wet substrate, making it unclear whether the regional environment was of a wet nature like Trinil or had a more arid character like Kedung Brubus. It was suggested that this dichotomy was the result of the chronologically mixed nature of the sample, containing specimens of the upper Kabuh formation, corresponding with the younger

and drier Kedung Brubus stage, and specimens from the Grenzbank, that can be correlated with the older and wetter Trinil (H.K.) stage.

These newly generated palaeoenvironmental reconstructions made an important contribution to our knowledge of the environmental context of *Homo erectus* in Southeast Asia. In East Java where this hominin species was present, regional environments were shown to be of a continually open nature. This was in line with the idea that *Homo erectus* was a species that depended on environments with an open vegetation structure and lends support to a scenario where its dispersal was fascilitated by the spread of open environments in Africa and Eurasia in the Plio-Pleistocene (Dennell & Roebroeks 2005, Dennell 2010).

This study cannot be considered as a *direct* test of the role of extrinsic or intrinsic factors in early hominin dispersal, but it does serve as a test whether the conditions were met to allow for a predominantly extrinsic explanation for this event in human evolution. Although the results of this thesis show that those conditions were fulfilled, there are also indications for a certain behavioural flexibility in *Homo erectus*. Despite the fact that most -if not all- *Homo erectus* sites tend to be of an open nature, the differences between conditions present at Trinil and Kedung Brubus (the latter being substantially drier than the former) were such that it can only by concluded that *Homo erectus* must have had a certain capacity to cope with changing environmental conditions. Upon closer inspection, the available palaeoecological data for other known *Homo erectus* sites corroborated this picture and confirmed that the species was found in a range of habitats, albeit confounded by the presence of an open vegetation structure.

Although this dissertation tried to make optimal use of new and existing palaeoecological data to address questions about early hominin behaviour, it should be remembered that our understanding of the palaeoenvironmental context of *Homo erectus* remains limited. Many

areas where this species was probably present at some point (e.g. Central Asia or West Africa) have barely received any attention from palaeoanthropologists. Even for other regions, where the presence of *Homo erectus* has already been attested (North Africa, Turkey), palaeoecological data often remain scarce (see Chapter 3.5). This makes the inferences made in this study, by necessity, of a generalized nature, but also leaves a number of directions for future research open.

A combination of further fieldwork in the unexplored regions of the purported *Homo erectus* range and new palaeoecological research on known sites, will help to fill in the gaps of a more solid and detailed palaeoenvironmental framework. New fieldwork would ideally also focus on refining the chronological framework, as correlating events in human evolution with climatic and environmental history is currently complicated by problems of timing (see e.g. Anton 2003, Anton & Swisher 2004). Renewed palaeoecological research would benefit from a multiproxy approach, where different methods, such as ecomorphology, palynology and isotope studies, can together provide a more holistic picture of regional environments that allows for uncomplicated inter-site comparisons. Such improvements would undoubtedly help to specify which ecological parameters played a role in limiting or facilitating *Homo erectus* dispersal. For Java specifically, future research should perhaps focus on the oldest and youngest stages associated with *Homo erectus*. The conditions surrounding Mojokerto are still a matter of debate (Huffman & Zaim 2003, Morwood *et al*. 2003, Anton & Swisher 2004, O'Connell & Desilva 2013, Morley *et al.* 2020) and about the younger Ngandong fossils (and the corresponding biostratigraphic stage) practically nothing is known (Huffman *et al*. 2010). These sites are, nevertheless, important as they can be informative the conditions that were present during the first appearance and final disappearance of *Homo erectus* in the region.

Methodologically there are also a number of directions in which this research can be taken. So far only a limited number of anatomical elements have been used in cervid ecomorphological

studies (Curran 2009, 2012, 2015, 2018, this study), but research on bovids has indicated that a number of other elements in the artiodactyl skeleton are also promising for further analysis (see Kovarovic & Andrews 2007). The other way around, bovids have more often been used in ecomorphological studies, but represent an interesting family on which the new methods developed in this thesis could be applied. Especially the use of GMM is still in its infancy and should be further developped as far as its application on artiodactyl bones is concerned. When developing such new models (for bovids as well as for cervids), increasing the sample size would be advisable, as this should lead to more robust results. A final angle that deserves further exploration, is the use of detailed georeferenced data in predictive models, where museum specimens with precise locality data can be correlated with specific environmental data (e.g. precipitation, tree cover, soil composition) available for those coordinates. Although museum specimens with such precise metadata are less common, models developed using this type of data could allow for much more detailed habitat reconstructions.

Ultimately this dissertation represents but a first step in the application of new methods to old problems. Considerable work remains to be done, improving our understanding of Early- and Middle Pleistocene environments and the way in which we conduct palaeoecological studies. This study focused on a number of specific sites to contextualize the behaviour and dispersal of *Homo erectus* in Southeast Asia. By successfully using newly developped ecomorphological methods to reconstruct hominin palaeoenvironments in Java, the notion was strengthened that identifying the environmental conditions surrounding our ancestors is imperative to understand their behaviour. Nevertheless, it was also shown that in order to understand such broad, overarching patterns in human evolution, it is necessary to combine data from multiple localities. Future palaeoanthropological research will have to take such an integrative approach, which will undoubtedly lead to exciting new insights in the decades to come.

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Appendix A: Habitat assignments

1. Habitat assignments: breakdown of number of species and specimens per habitat/locomotor group.

	Calcaneus		Intermediate phalanx	
	N (specimens)	N (species)	N (specimens)	N (species)
Type 1	56	8	47	7
Type 2	9	5	11	5
Type 3	33	7	40	7
Type 4	7	5	10	5
Type 5	20	4	20	4
Type 6	-	-	14	1
Total:	125	26	142	29

Appendix B: Extant specimens

Taxon	Institute	Coll. number	Sp. code	Provenance	Sex	Calc	Ph2
Axis axis	KBIN	1297s	AXA	India	f	x	x
Axis axis	KBIN	1297y	AXA	India	f	x	x
Axis axis	KBIN	3719	AXA		f	x	x
Axis axis	KBIN	7499	AXA		m	x	x
Axis axis	KBIN	7599	AXA		f	x	x
Axis axis	KBIN	1297e	AXA	Zoo Brussels	f	x	
Axis axis	KBIN	3706	AXA		f	x	
Axis axis	KBIN	3707	AXA		f	x	
Axis axis	KBIN	3720	AXA		f	x	x
Axis axis	RMNH	43556	AXA	Bengal, India	m	x	x
Axis axis	RMNH	43557	AXA	Bengal, India	f	x	x
Axis axis	KBIN	1297e	AXA	Zoo Brussels	f		x
Axis axis	KBIN	3703	AXA				x
Axis (*Hyelaphus*) *kuhlii*	RMNH	10605a	AXK	Bawean, Indonesia	m	x	x
Axis (*Hyelaphus*) *kuhlii*	RMNH	43559	AXK	Bawean, Indonesia	m	x	x
Axis (*Hyelaphus*) *kuhlii*	RMNH	43558	AXK	Bawean, Indonesia	m		x
Cervus (*Przewalskium*) *albirostris*	MNHN	2011895	CEA				x
Alces alces	KBIN	1287c	ALA		m	x	x
Alces alces	KBIN	18068	ALA		m	x	x
Alces alces	MFN	77296	ALA	*			x
Alces alces	UWBM	39479	ALA	Canada**		x	x
Alces alces	KBIN	1287b	ALA		f	x	
Alces alces	KBIN	16402	ALA	Zoo Antwerp	m	x	x
Alces alces	KBIN	1287b	ALA		f		x
Capreolus capreolus	KBIN	1173	CAC	Belgium	m	x	
Capreolus capreolus	KBIN	1285b	CAC	Bouillon, Belgium	f	x	x
Capreolus capreolus	KBIN	13353	CAC		f	x	x
Capreolus capreolus	KBIN	14891	CAC		f	x	x
Capreolus capreolus	KBIN	33479	CAC	Zonienwoud, Belgium	m	x	x
Capreolus capreolus	KBIN	34543	CAC	Waals Brabant, Belgium	f	x	x
Capreolus capreolus	KBIN	34561	CAC	La Reid, Liège, Belgium	f	x	
Capreolus capreolus	KBIN	37267	CAC	Theux, Liège, Belgium	f	x	x
Capreolus capreolus	KBIN	39037	CAC	Theux, Liège, Belgium	m	x	x
Capreolus capreolus	ULILLE	782	CAC	France	f	x	x
Capreolus capreolus	KBIN	7753	CAC	Haute Lesse, Belgium	m	x	
Capreolus capreolus	KBIN	15870	CAC	Norway	f	x	x
Capreolus capreolus	KBIN	17191	CAC	Zoo Antwerp	f	x	
Capreolus capreolus	KBIN	17472	CAC	Zoo Antwerp	f	x	x
Capreolus capreolus	CAR	b057	CAC	Belgium	f	x	x
Capreolus capreolus	ULILLE	cc002	CAC	France	f	x	x
Capreolus capreolus	KBIN	15639	CAC				x
Capreolus capreolus	NMR	999000002020	CAC				x
Capreolus capreolus	NMR	999000002022	CAC				x
Capreolus capreolus	CAR	b056	CAC	Belgium	f		x

Taxon	Institute	Coll. number	Sp. code	Provenance	Sex	Calc	Ph2
Cervus canadensis	MNHN	1897346	CCA		f	x	
Cervus canadensis	KBIN	3718	CCA		f	x	x
Cervus canadensis	KBIN	3977	CCA		m	x	
Cervus canadensis	IMNH	r749	CCA	Canada**	f	x	x
Cervus canadensis	KBIN	3897	CCA	Canada	f		x
Cervus canadensis	KBIN	3716	CCA	zoo Antwerp	f		x
Cervus canadensis	KBIN	3977	CCA	zoo Antwerp	m		x
Cervus elaphus	KBIN	1174	CEE	Neupont, Belgium	m	x	x
Cervus elaphus	KBIN	1307y	CEE		f	x	x
Cervus elaphus	MPIEVA	501	CEE	*	m	x	x
Cervus elaphus	RMNH	6958	CEE	Lisse, The Netherlands			x
Cervus elaphus	ULILLE	ce001	CEE	France	f	x	x
Cervus elaphus	ULILLE	ce002	CEE	France	f	x	
Cervus elaphus	ULILLE	ce003	CEE	France		x	
Cervus elaphus	KBIN	3704	CEE		m	x	x
Cervus elaphus	Ul	1082	CEE	Belgium		x	x
Cervus elaphus	Ul	1082e	CEE	Belgium		x	x
Cervus elaphus	Ul	15143	CEE	Belgium		x	
Cervus elaphus	CAR	ce001	CEE	Belgium			x
Elaphodus cephalopus	MNHN	1896689	ELC	Setchuan, China		x	x
Elaphodus cephalopus	AMNH	114551	ELC				x
Elaphodus cephalopus	AMNH	84462	ELC			x	x
Elaphodus cephalopus	AMNH	84463	ELC				x
Elaphodus cephalopus	AMNH	115638	ELC			x	
Cervus nippon	RMNH	25990	CEN	Japan	m	x	x
Cervus nippon	RMNH	25991	CEN	Japan	m	x	x
Dama dama	KBIN	2255	DDA	Namur, Belgium	m	x	x
Dama dama	KBIN	2256	DDA	Namur, Belgium	m	x	x
Dama dama	KBIN	2256a	DDA	Namur, Belgium	f	x	x
Dama dama	KBIN	2258	DDA	Namur, Belgium	m	x	x
Dama dama	KBIN	3709	DDA	Namur, Belgium	m	x	x
Dama dama	KBIN	3710	DDA	Namur, Belgium	f	x	x
Dama dama	CAR	dd001	DDA	Belgium	f	x	x
Dama dama	KBIN	2254	DDA	Villers-sur-Lesse, Belgium	m	x	x
Dama dama	KBIN	1310b	DDA	Limerick, Ireland	m	x	x
Dama dama	ULILLE	dd001	DDA	France	f	x	x
Dama dama	RMNH	51506	DDA			x	x
Cervus (*Elaphurus*) *davidianus*	MNHN	197392	ELD			x	x
Cervus (*Elaphurus*) *davidianus*	KBIN	15252	ELD	Zoo Antwerp	m	x	x
Cervus (*Elaphurus*) *davidianus*	MNHN	19662	ELD			x	x
Cervus (*Panolia*) *eldii*	MNHN	1937157	CEL		f		x
Cervus (*Panolia*) *eldii*	RMNH	11415	CEL	Diergaarden Blijdorp zoo	f	x	
Cervus (*Panolia*) *eldii*	MNHN	201322	CEL	France (Captive)	m	x	x
Cervus (*Panolia*) *eldii*	MNHN	2011190	CEL				x
Cervus (*Panolia*) *eldii*	MNHN	2011191	CEL	France (Captive)			x

Taxon	Institute	Coll. number	Sp. code	Provenance	Sex	Calc	Ph2
Hippocamelus antisensis	MNHN	19571303	HIA	Putina, Puno, Peru	f		x
Axis (*Hyelaphus*) *porcinus*	KBIN	1299	AXP		f	x	x
Axis (*Hyelaphus*) *porcinus*	KBIN	1299y	AXP		f	x	x
Axis (*Hyelaphus*) *porcinus*	KBIN	3700	AXP		m	x	x
Axis (*Hyelaphus*) *porcinus*	MNHN	197172	AXP	Vietnam	f	x	x
Axis (*Hyelaphus*) *porcinus*	MNHN	1908531	AXP				x
Hydropotes inermis	MNHN	194887	HYI		f	x	x
Hydropotes inermis	MNHN	197136	HYI	China	m	x	
Hydropotes inermis	KBIN	12153	HYI	Zoo Antwerp	m	x	x
Hydropotes inermis	KBIN	15510	HYI	Zoo Antwerp	f	x	x
Hydropotes inermis	MNHN	1935118	HYI			x	
Hydropotes inermis	MNHN	1962323	HYI		m	x	x
Hydropotes inermis	MNHN	1992403	HYI	Zoo Vincennes	m	x	x
Hydropotes inermis	MNHN	a9994	HYI			x	
Hydropotes inermis	MNHN	nr001	HYI			x	x
Hydropotes inermis	KBIN	197136	HYI	China	m	x	x
Hydropotes inermis	KBIN	14221	HYI	Zoo Antwerp	m	x	x
Mazama gouazoubira	MNHN	1981687	MAG	French Guyana	m		x
Mazama americana	RMNH	43562	MAA	"America"	f	x	x
Mazama americana rufa	RMNH	51209a	MAA	Surinam	m		x
Mazama americana rufa	RMNH	51238a	MAA	Brazil	f		x
Mazama americana	KBIN	1473	MAA	Zoo Antwerp	m	x	
Mazama americana	RMNH	51237	MAA	Surinam	f		x
Mazama americana	MNHN	1971285	MAA		f		x
Muntiacus reevesi	MNHN	198543	MUR	Zoo Paris	f	x	x
Muntiacus reevesi	CAR	B057b	MUR	Belgium (feral)	f	x	x
Muntiacus reevesi	MNHN	194912	MUR	Zoo Paris		x	x
Muntiacus muntjak	KBIN	3705	MUM		m	x	x
Muntiacus muntjak	MNHN	197936	MUM			x	x
Muntiacus muntjak	MNHN	185662	MUM		m	x	x
Muntiacus muntjak	MNHN	1992379	MUM				x
Muntiacus muntjak	RMNH	51384	MUM	Java, Indonesia	f	x	x
Muntiacus muntjak	MNHN	1909442	MUM				x
Odocoileus virginianus leucurus	KBIN	7755	ODV	Zoo Antwerp	m	x	x
Odocoileus virginianus	KBIN	9746	ODV	New York, United States	f	x	x
Odocoileus virginianus	KBIN	39526	ODV		m	x	x
Odocoileus hemionus	IMNH	r146	ODH	United States**		x	x
Odocoileus hemionus	IMNH	r2093	ODH	United States**		x	
Odocoileus hemionus	MNHN	nonr002	ODH				x
Ozotoceros bezoarticus	RMNH	51320	OZB	South East Brazil	m	x	x
Pudu mephistophiles	USNM	92167	PUM			x	
Pudu mephistophiles	USNM	282141	PUM			x	x
Pudu mephistophiles	USNM	309045	PUM				x
Pudu puda	KBIN	21137	PUP	Zoo Antwerp	f	x	
Pudu puda	KBIN	36522	PUP	Zoo Antwerp	m	x	x
Pudu puda	KBIN	39041	PUP	Zoo Antwerp	f	x	
Pudu puda	MNHN	2006501	PUP	Zoo Paris	m	x	x
Pudu puda	MNHN	19981956	PUP	Zoo Paris	m	x	x

Taxon	Institute	Coll. number	Sp. code	Provenance	Sex	Calc	Ph2
Cervus (*Rusa*) *alfredi*	MNHN	ra01	CAL		m		x
Cervus (*Rusa*) *alfredi*	MNHN	ra02	CAL		m	x	x
Rangifer tarandus	CMC	f11378	RAT	Canada**		x	x
Rangifer tarandus	KBIN	3731	RAT		f	x	
Rangifer tarandus	KBIN	6327	RAT		f	x	x
Rangifer tarandus	KBIN	7497	RAT			x	x
Rangifer tarandus	ASM	nnr7	RAT	*	m		x
Rangifer tarandus	KBIN	1290e	RAT	Zoo Brussels	f	x	x
Rangifer tarandus	KBIN	1290g	RAT		m	x	x
Rangifer tarandus	KBIN	3702	RAT		m	x	x
Rangifer tarandus	KBIN	16936	RAT		m	x	x
Rangifer tarandus	KBIN	17192	RAT		f	x	x
Rangifer tarandus	MNHN	194529	RAT			x	x
Rangifer tarandus	Persbodibratlund	nnr1	RAT	Sweden*		x	x
Rangifer tarandus	Ul	4350	RAT			x	x
Rangifer tarandus	KBIN	7496	RAT	Zoo Antwerp	m		x
Rangifer tarandus	MNHN	vl1200	RAT				x
Cervus (*Rusa*) *timorensis*	KBIN	1303d	CET	Indonesia	m	x	x
Cervus (*Rusa*) *timorensis*	RMNH	43496	CET			x	x
Cervus (*Rusa*) *timorensis*	MNHN	18793036	CET	Zoo Paris			x
Cervus (*Rusa*) *timorensis*	MNHN	129744	CET				x
Cervus (*Rusa*) *timorensis*	MNHN	1886366	CET				x
Cervus (*Rusa*) *unicolor*	KBIN	7500	CEU		f	x	x
Cervus (*Rusa*) *unicolor*	RMNH	43544	CEU	Indonesia	f	x	x
Cervus (*Rusa*) *unicolor*	KBIN	1300	CEU	Zoo Brussels	m	x	x
Cervus (*Rusa*) *unicolor*	RMNH	41452	CEU	Borneo	m		x
Cervus (*Rusa*) *unicolor*	MNHN	1878425	CEU				x
Cervus (*Rusa*) *unicolor*	MNHN	1879222	CEU				x
Cervus (*Rusa*) *marianna*	MNHN	1854221	CEM		f	x	x

-Specimens with a star (*) were shared as 3D scans by the Max Planck Institute of Evolutionary Anthropology (Leipzig, Germany) (Niven et al. 2009), specimens with two stars (**) by the Virtual Zooarchaeology of the Arctic project (Idaho University, U.S.) (Maschner et al. 2011, Betts et al. 2011).

Institute acronyms:

AMNH= American Museum of Natural History, New York, U.S.
ASM= Anatomische Staatssamlung München, München, Germany
CAR= Center for Artefact Research vzw, Mechelen, Belgium
CMC=Canadian Museum of History, Gatineau, Canada
IMNH= Idaho Museum of Natural History, Pocatello, U.S.
KBIN=Royal Belgian Institute of Natural Sciences, Brussels, Belgium
MFN= Museum für Naturkunde, Berlin, Germany
MNHN= Muséum National d'Histoire Naturelle, Paris, France
MPIEVA= Max Planck Institute of Evolutionary Anthropology, Leipzig, Germany
NMR= Natural History Museum Rotterdam, Rotterdam, The Netherlands
Persbodibratlund= Personal collection Bodi Bratlund, Sweden
RMNH= Naturalis Biodiversity Center, Leiden (formerly Rijksmuseum Natuurlijke Historie), The Netherlands
Ul= Université de Liège (Palaeontology Service), Liège, Belgium
ULILLE= Université Charles-de-Gaule Lille III (Zooarchaeology laboratory), Lille, France
USNM= National Museum of Natural History, Washington D.C., U.S.
UWBM= University of Washington Burke Museum, Seattle, U.S.

Appendix C: Fossil specimens

Taxon	Institute	Collection	Coll. number	Sp. code	Provenance	Element
Cervus kendengensis	RMNH	Dubois	5409	CKE	Java	calc
Cervus kendengensis	RMNH	Dubois	5889	CKE	Java	calc
Cervus kendengensis	RMNH	Dubois	6438	CKE	Bangle	calc
Cervus kendengensis	RMNH	Dubois	6441	CKE	Java	calc
Cervus kendengensis	RMNH	Stehn & Umbgrove	j2035	CKE	Banuraja	calc
Cervus kendengensis	RMNH	Dubois	nonr	CKE	Java	calc
Cervus kendengensis	RMNH	Dubois	6480	CKE	Java	Ph2
Cervus kendengensis	RMNH	Dubois	6257	CKE	Java	Ph2
Cervus kendengensis	RMNH	Dubois	6972	CKE	Kedung Brubus	Ph2
Cervus kendengensis	RMNH	Dubois	8697	CKE	Kedung Brubus	Ph2
Axis lydekkeri	RMNH	Dubois	nonr1	ALY	Java	calc
Axis lydekkeri	RMNH	Dubois	nonr2	ALY	Java	calc
Axis lydekkeri	RMNH	Dubois	5648	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	5649	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	5651	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	5652	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	5952	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois.	5998	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6045	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6046	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6049	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6149	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6150	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6156	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6157	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6160	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6867	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6880	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6881	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6884	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6885	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6886	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	6887	ALY	Trinil	calc
Axis lydekkeri	RMNH	Dubois	10958	ALY	Java	calc
Axis lydekkeri	MFN	Selenka	22490	ALY	Trinil	calc
Axis lydekkeri	MFN	Selenka	22491	ALY	Trinil	calc
Axis lydekkeri	MFN	Selenka	22492	ALY	Trinil	calc
Axis lydekkeri	MFN	Selenka	22493	ALY	Trinil	calc
Axis lydekkeri	MFN	Selenka	22495	ALY	Trinil	calc
Axis lydekkeri	MFN	Selenka	22496	ALY	Trinil	calc
Axis lydekkeri	MFN	Selenka	22497	ALY	Trinil	calc

Taxon	Institute	Collection	Coll. number	Sp. code	Provenance	Element
Axis lydekkeri	RMNH	Dubois	1575g	ALY	Butak	Ph2
Axis lydekkeri	RMNH	Dubois	5918e	ALY	Trinil	Ph2
Axis lydekkeri	RMNH	Dubois	13322	ALY	Java	Ph2
Axis lydekkeri	RMNH	Dubois	nonr1	ALY	Java	Ph2
Axis lydekkeri	RMNH	Dubois	nonr2	ALY	Java	Ph2
Axis lydekkeri	RMNH	Dubois	nonr3	ALY	Java	Ph2
Axis lydekkeri	RMNH	Dubois	nonr4	ALY	Java	Ph2
Axis lydekkeri	RMNH	Dubois	5918a	ALY	Trinil	Ph2
Axis lydekkeri	RMNH	Dubois	13324	ALY	Java	Ph2
Axis lydekkeri	RMNH	Dubois	5918b	ALY	Trinil	Ph2
Axis lydekkeri	RMNH	Dubois	5918d	ALY	Trinil	Ph2
Axis lydekkeri	RMNH	Dubois	6245d	ALY	Trinil	Ph2
Axis lydekkeri	RMNH	Dubois	5918f	ALY	Trinil	Ph2
Axis lydekkeri	RMNH	Dubois	5918i	ALY	Trinil	Ph2
Axis lydekkeri	MFN	Selenka	22447	ALY	Trinil	Ph2
Axis lydekkeri	MFN	Selenka	22448	ALY	Trinil	Ph2
Axis lydekkeri	MFN	Selenka	22635	ALY	Trinil	Ph2
Axis lydekkeri	MFN	Selenka	22636	ALY	Trinil	Ph2
Axis lydekkeri	MFN	Selenka	22641	ALY	Trinil	Ph2
Axis lydekkeri	MFN	Selenka	22642	ALY	Trinil	Ph2
Axis lydekkeri	MFN	Selenka	22643	ALY	Trinil	Ph2
Axis lydekkeri	MFN	Selenka	22644	ALY	Trinil	Ph2
Cervidae indet.	GMB	Watanabe & Kadar	sa240178a	CSP	Sangiran	calc
Cervidae indet.	GMB	Watanabe & Kadar	sa240178b	CSP	Sangiran	calc
Cervidae indet.	GMB	Watanabe & Kadar	sa250178	CSP	Sangiran	calc
Cervidae indet.	GMB	Watanabe & Kadar	sa250878	CSP	Sangiran	calc
Cervidae indet.	GMB	Watanabe & Kadar	sa11087849	CSP	Sangiran	calc
Cervidae indet.	GMB	Watanabe & Kadar	sa1401791	CSP	Sangiran	calc
Cervidae indet.	GMB	Aziz	sem0405193e	CSP	Sembungan	calc
Cervidae indet.	GMB	Watanabe & Kadar	sa060877	CSP	Sangiran	calc
Cervidae indet.	GMB	Watanabe & Kadar	sa170378	CSP	Sangiran	calc
Cervidae indet.	GMB	Watanabe & Kadar	nonr1	CSP	Sangiran	calc
Cervidae indet.	GMB	Watanabe & Kadar	sa140878	CSP	Sangiran	ph2
Cervidae indet.	GMB	Watanabe & Kadar	sa240779	CSP	Sangiran	ph2
Cervidae indet.	GMB	Watanabe & Kadar	sa240779a	CSP	Sangiran	ph2
Cervidae indet.	GMB	Watanabe & Kadar	sa910104	CSP	Sangiran	ph2
Cervidae indet.	GMB	Watanabe & Kadar	sa18087940	CSP	Sangiran	ph2
Cervidae indet.	GMB	Watanabe & Kadar	sa1261177	CSP	Sangiran	ph2
Cervidae indet.	GMB	Watanabe & Kadar	sa-nr16	CSP	Sangiran	ph2

Institute acronyms:

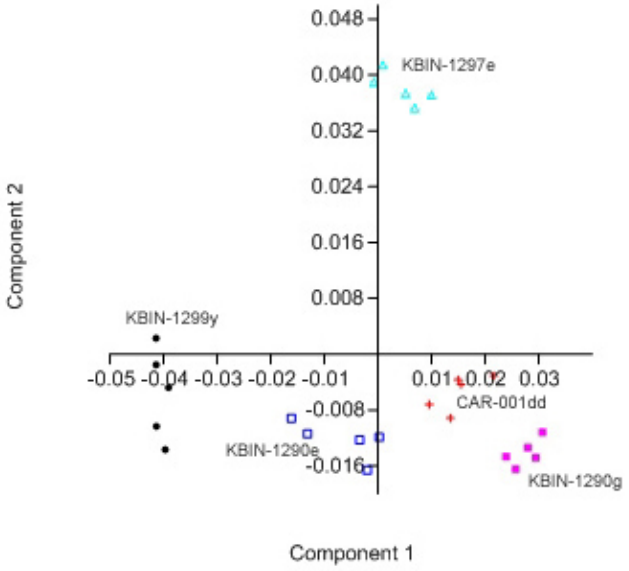
GMB= Geological Museum Bandung, Bandung, Indonesia

MFN= Museum für Naturkunde, Berlin, Germany

RMNH= Naturalis Biodiversity Center, Leiden (formerly Rijksmuseum Natuurlijke Historie), The Netherlands

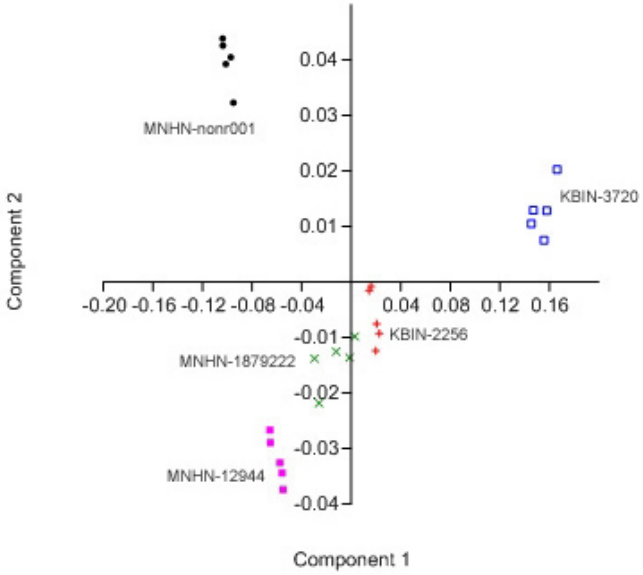
Appendix D: Results error tests

1. Scatterplot resulting from (standard) PCA conducted on five re-scanned replicates of five cervid calcanei (KBIN 1290e (*Rangifer tarandus*), KBIN 1290g (*Rangifer tarandus*), CAR dd001 (*Dama dama*), KBIN 1297e (*Axis axis*) and KBIN 1297y (*Axis porcinus*)). Eigenvalues are given for the first ten PC's.



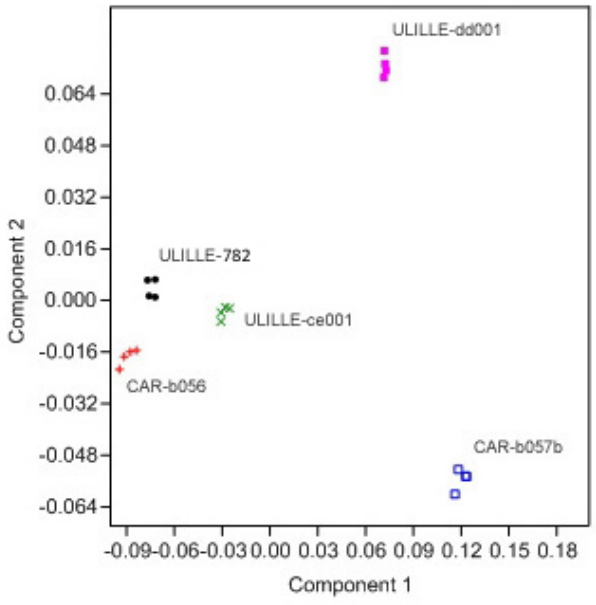
PC	Eigenvalue	% variance
1	0,000574349	47.009
2	0,000391785	32.067
3	0.000129605	10.608
4	5.68E-05	4.6487
5	2.43E-05	1.9859
6	1.66E-05	1.3557
7	1.55E-05	1.2673
8	6.49E-06	0.53125
9	4.29E-06	0.35126
10	1.71E-06	0.14002

2. Scatterplot resulting from (standard) PCA conducted on five re-scanned replicates of five cervid intermediate phalanges (MNHN 1879222 (*Cervus unicolor*), MNHN 129744 (*Cervus timorensis*), KBIN 2256 (*Dama dama*), MNHN nonr001 (*Hydropotes inermis*) and KBIN 3720 (*Axis axis*)). Eigenvalues are given for the first ten PC's.



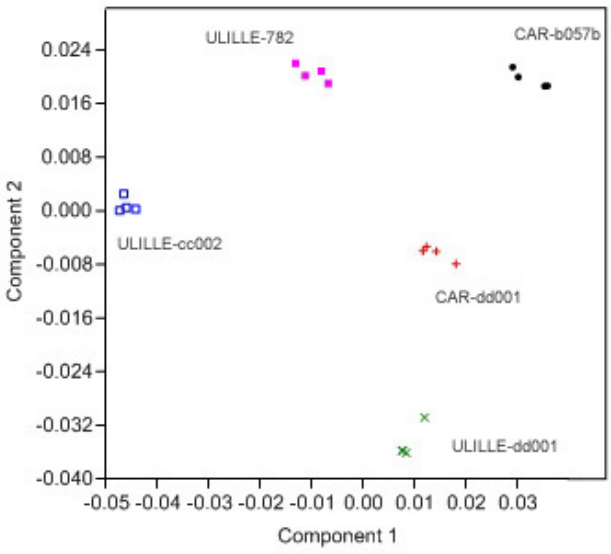
PC	Eigenvalue	% variance
1	0.00796721	84.648
2	0.000644419	6.8467
3	0,00035124	3,7318
4	0,00026154	2,7787
5	5,02E-05	0,53334
6	3,60E-05	0,38231
7	3,34E-05	0,3549
8	1.84E-05	0,19532
9	1,42E-05	0,15098
10	9,29E-06	0,098658

3. Scatterplot resulting from (standard) PCA conducted on four landmarking replicates of five cervid intermediate phalanges (CAR b056 (*Capreolus capreolus*), CAR b057b (*Muntiacus reevesi*), ULILLE 782 (*Capreolus capreolus*), ULILLE DD001 (*Dama dama*), ULILLE CE001 (*Cervus elaphus*)), used as intra-observer error test. Eigenvalues are given for the first ten PC's.



PC	Eigenvalue	% variance
1	0.0071574	68.343
2	0.0018417	17.586
3	0.000831463	79.393
4	0.000511559	48.847
5	0.0000370019	0.35332
6	0.0000307411	0.29353
7	0.0000196909	0.18802
8	0.0000184088	0.17578
9	0.00000984703	0.094025
10	0.00000563906	0.053845

4. Scatterplot resulting from (standard) PCA conducted on four landmarking replicates of five cervid intermediate phalanges (ULILLE 782 (*Capreolus capreolus*), ULILLE CC002 (*Capreolus capreolus*), ULILLE DD001 (*Dama dama*), CAR b057b (*Muntiacus reevesi*), CAR DD001 (*Dama dama*)), used as intra-observer error test. Eigenvalues are given for the first ten PC's.

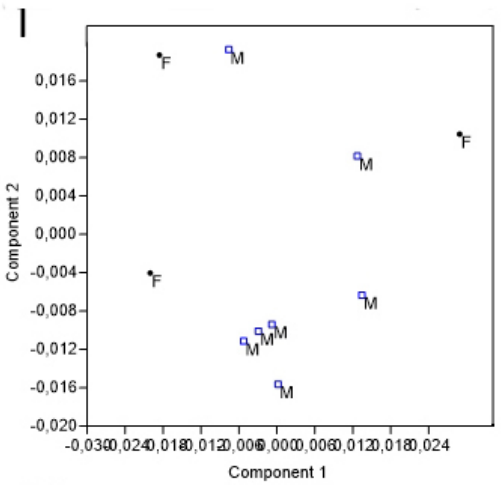


PC	Eigenvalue	% variance
1	0.000752706	52.435
2	0.000432928	30.158
3	0.000131978	91.938
4	0.0000936725	65.254
5	0.0000129375	0.90124
6	0.00000534817	0.37256
7	0.00000229386	0.15979
8	0.00000206831	0.14408
9	0.000000622547	0.043367
10	0.00000055504	0.038665

Appendix E: Results test sexual dimorphism

1. Results PCA (I) on group of ten *D. dama* calcanei to assess sexual dimorphism, with eigenvalues (II), broken stick model of eigenvalues (IV) and pairwise comparisons of an NPMANOVA on PC1 to PC4 (III). (M=male, F=female)

I



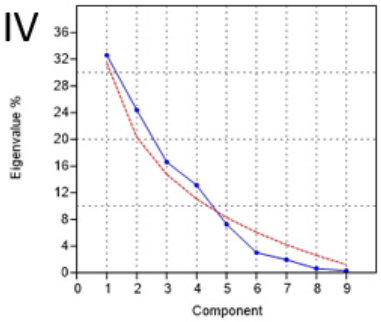
II

PC	Eigenvalue	% variance
1	0.000224474	32.644
2	0.000167833	24.407
3	0.00011419	16.606
4	9.01665E-05	13.112
5	5.00458E-05	7.2779
6	2.07115E-05	3.012
7	1.35119E-05	1.965
8	4.45987E-06	0.64857
9	2.24975E-06	0.32717

III

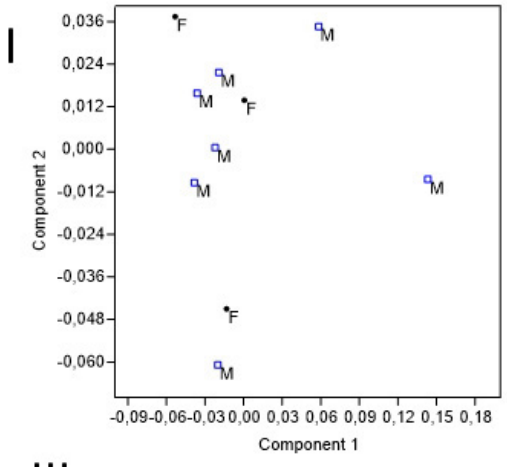
	M	F
M	-	0.734
F	0.734	-

IV



2. Results PCA (I) on group of ten *D. dama* phalanges to assess sexual dimorphism, with eigenvalues (II), broken stick model of eigenvalues (IV) and pairwise comparisons of an NPMANOVA on PC1 to PC4 (III). (M=male, F=female)

I



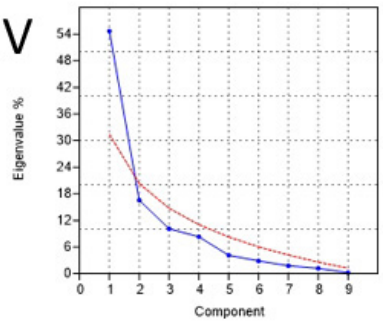
II

PC	Eigenvalue	% variance
1	0,00344227	54,698
2	0,00104313	16,575
3	0,000638088	10,139
4	0,000523716	8,3219
5	0,000261835	4,1606
6	0,000181533	2,8846
7	0,000112549	1,7884
8	7,54E-05	1,1984
9	1,47E-05	0,23365

III

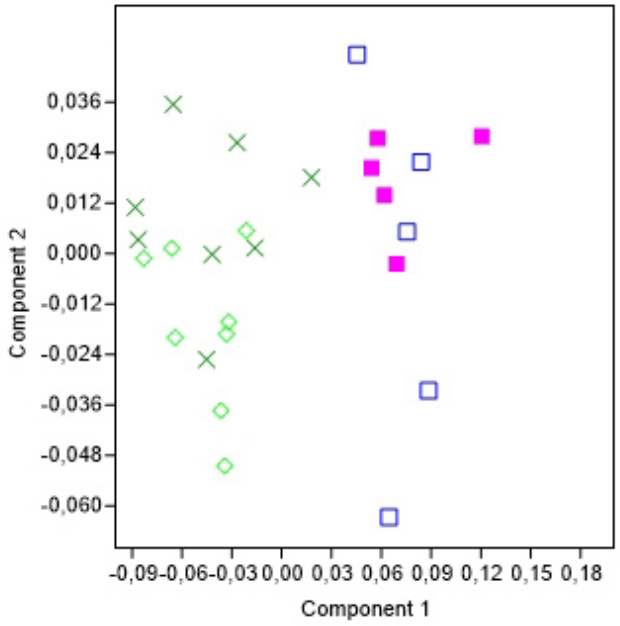
	F	M
F	-	0.6677
M	0,6677	-

IV



Appendix F: Results test difference anterior and posterior phalanges

1. Scatterplot of a (between groups) PCA on a dataset of 16 intermediate phalanges (eight anterior and eight posterior) belonging to *Capreolus capreolus* and 10 intermediate phalanges (5 anterior and 5 posterior) belonging to *Dama dama* to test for differences between forelimb and hindlimb specimens. With eigenvalues provided for PC's 1 to 4.



PC	Eigenvalue	% variance
1	0.0040864	74.271
2	0.000826542	15.023
3	0.000384902	6.9957
4	0.000204161	3.7107

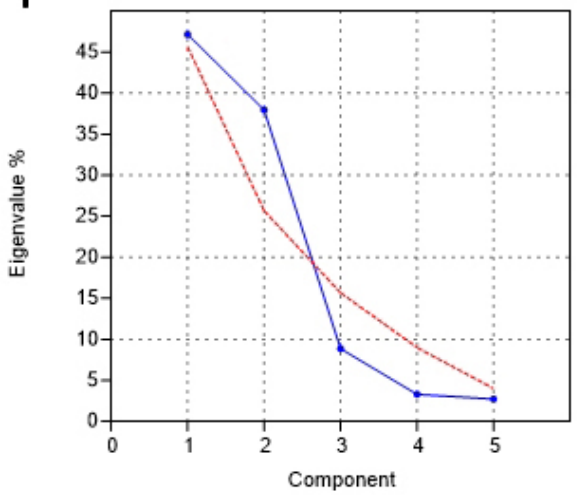
2. Pairwise comparisons of NPMANOVA on components 1 to 4 of a (between groups) PCA on anterior and posterior *C. capreolus* and *D. dama* specimens, with significant differences in bold.

	D. dama anterior	*D. dama* posterior	*C. capreolus* anterior	*C. capreolus* posterior
D. dama anterior	-	0.1755	**0.0008**	**0.0007**
D. dama posterior	0.1755	-	**0.001**	**0.001**
C. capreolus anterior	**0.0008**	**0.001**	-	0.0658
C. capreolus posterior	**0.0007**	**0.001**	0.0658	-

Appendix G: Eigenvalues associated with bg-PCA on all extant specimens

1. Eigenvalues associated with bg-PCA on all extant intermediate phalanges (II), with broken stick model of eigenvalue distributions (I).

I

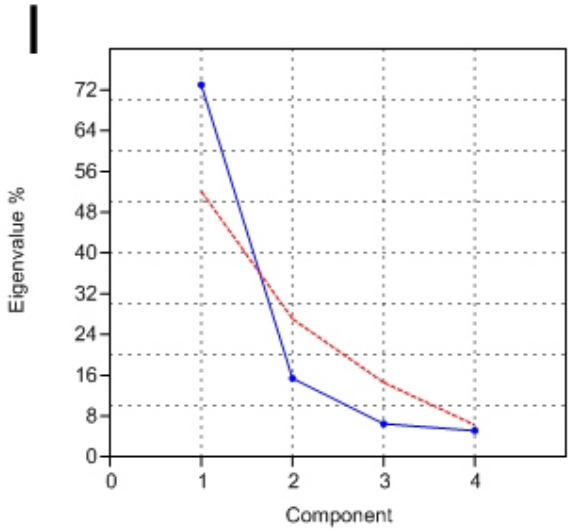


II

PC	Eigenvalue	% variance
1	0.00119212	47.151
2	0.000959776	37.961
3	0.000224192	8.8673
4	8.33E-05	3.2953
5	6.89E-05	2.7255

2. Eigenvalues associated with bg-PCA on all extant calcanei (II), with broken stick model of eigenvalue distributions (I).

I

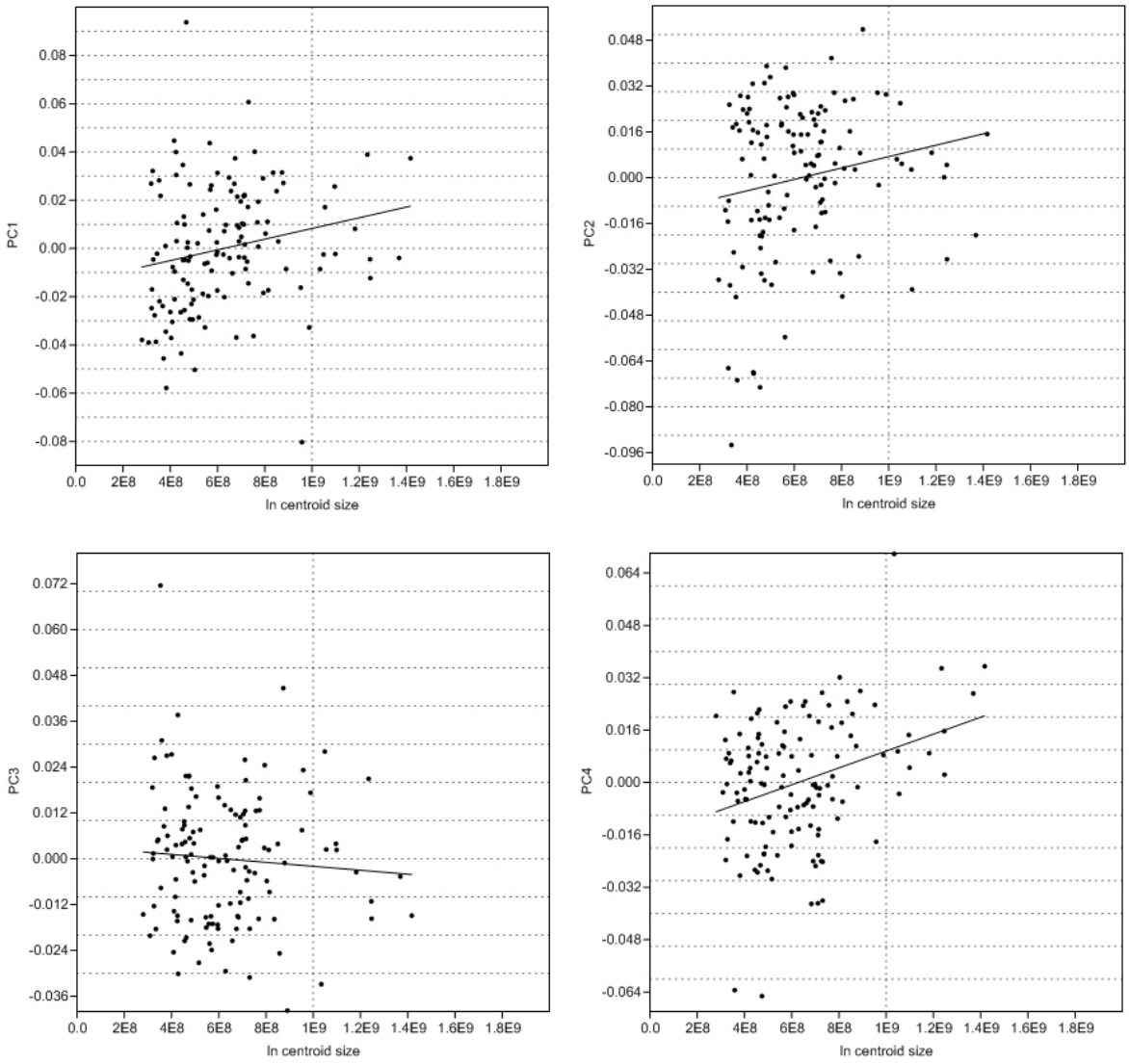


II

PC	Eigenvalue	% variance
1	0.000623456	73.007
2	0.000131479	15.396
3	5.52E-05	6.4584
4	4.39E-05	5.1379

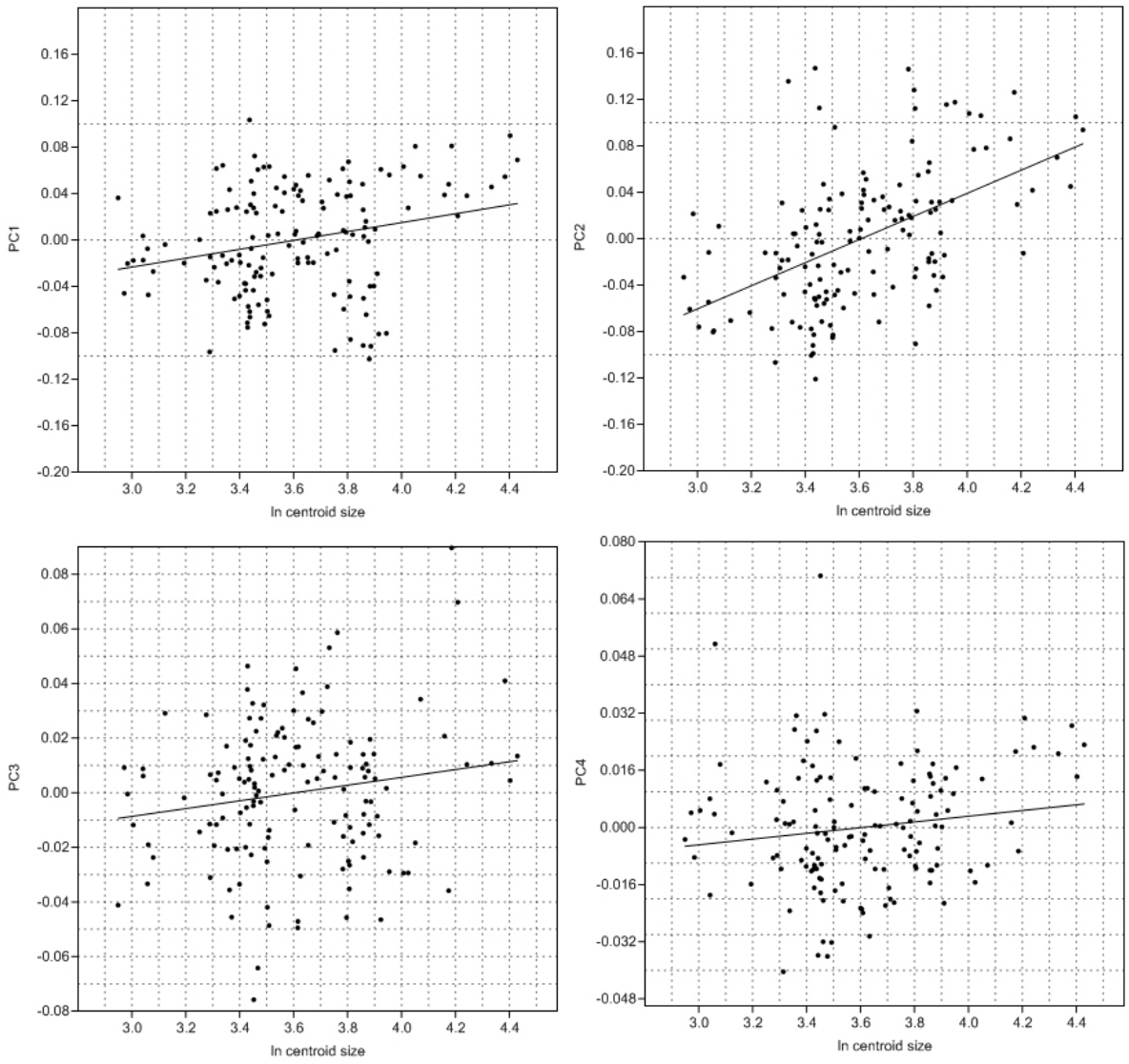
Appendix H: Regressions of relevant principal components against log centroid size

1. Results of ordinary least squares regressions of the first four principal components against log centroid size for all extant calcanei.



PC1		PC2		PC3		PC4	
R^2	0.0414	R^2	0.0306	R^2	0.005	R^2	0.0975
R	0.2035	R	0.17516	R	-0.71336	R	0.31231
p	0.0202	*p*	0.0462	*p*	0.4199	*p*	0.00029

2. Results of ordinary least squares regressions of the first four principal components against log centroid size for all extant intermediate phalanges.



PC1		PC2		PC3		PC4	
R^2	0.0629	R^2	0.2579	R^2	0.0276	R^2	0.0199
R	0.2508	R	0.5078	R	0.1662	R	0.1413
p	0.0026	*p*	<0.001	*p*	0.0488	*p*	0.0946

Appendix I: R-scripts and output data of PGLS regressions in Caper on the relevant principal components

1. R-scripts and output of PGLS regression on relevant components of a PCA on all extant calcanei.

Script:

```
cerviddata<-read.table("C:\\Users\\Userone\\Desktop\\calcaneus\\cerviddata.txt, header = TRUE)

cervidtree<-read.nexus("C:\\Users\\Userone\\Desktop\\ calcaneus \\cervidtree.nex")

cervid<- comparative.data(phy = cervidtree, data = cerviddata, names.col = Species, vcv = TRUE, na.omit = FALSE, warn.dropped = TRUE)

model.pgls<-pgls(PC1+PC2+PC3+PC4+PC5~factor(habitat), data = cervid, lambda ="ML", bounds = list(lambda=c(0.001,1), kappa=c(1e-6,3), delta=c(1e-6,3)))

summary(model.pgls)
```

Output:

Call:

```
pgls(formula = PC1 + PC2 + PC3 + PC4 + PC5 ~ factor(habitat),

    data = cervid, lambda = "ML", bounds = list(lambda = c(0.001,

        1), kappa = c(1e-06, 3), delta = c(1e-06, 3)))
```

Residuals:

```
     Min       1Q   Median       3Q      Max

-0.41509 -0.20067 -0.03795  0.15045  0.52727
```

Branch length transformations:

```
kappa  [Fix]  : 1.000

lambda [ ML]  : 0.906

  lower bound : 0.001, p = 0.3227

  upper bound : 1.000, p = 0.29021

  95.0% CI   : (0.218, NA)

delta  [Fix]  : 1.000
```

Coefficients:

```
                Estimate Std. Error t value Pr(>|t|)

(Intercept)       -0.0093037  0.0391663 -0.2375   0.8148
```

factor(habitat)for -0.0232979 0.0386020 -0.6035   0.5533

factor(habitat)gra -0.0137229 0.0362072 -0.3790   0.7089

factor(habitat)mou 0.0315348 0.0445770 0.7074   0.4879

factor(habitat)tun -0.0347755 0.0753348 -0.4616   0.6496

factor(habitat)woo 0.0446740 0.0362310 1.2330   0.2326

Residual standard error: 0.2994 on 19 degrees of freedom

Multiple R-squared: 0.283, Adjusted R-squared: 0.09431

F-statistic: 1.5 on 5 and 19 DF, p-value: 0.2366

2. R-scripts and output of PGLS regression on relevant components of a PCA on all extant intermediate phalanges.

Script:

```
NHIS<-read.table("C:\\Users\\Userone\\Desktop\\Phalanges\\cerviddata.txt ",header=TRUE)

NHIS<-read.nexus("C:\\Users\\Userone\\Desktop\\Phalanges\\cervidtree.nex ")

NHIS<- comparative.data(phy = cervidtree, data = cerviddata, names.col = Species, vcv.dim=3, vcv = TRUE, na.omit = FALSE, warn.dropped = TRUE)

model.pgls<-pgls(PC1+PC2+PC3+PC4~factor(habitat), data = cervid, lambda ="ML", bounds = list(lambda=c(0.001,1), kappa=c(1e-6,3), delta=c(1e-6,3)))

summary(model.pgls)
```

Output:

Call:

```
pgls(formula = PC1 + PC2 + PC3 + PC4 ~ factor(habitat), data = cervid,

   lambda = "ML", bounds = list(lambda = c(0.001, 1), kappa = c(1e-06,

      3), delta = c(1e-06, 3)))
```

Residuals:

```
    Min      1Q  Median      3Q     Max

-0.50537 -0.12803  0.08418  0.26392  0.53630
```

Branch length transformations:

kappa [Fix] : 1.000

lambda [ML] : 0.811

lower bound : 0.001, p = 0.072579

upper bound : 1.000, p = 0.066754

95.0% CI : (NA, NA)

delta [Fix] : 1.000

Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.0209160	0.0442900	-0.4723	0.6421
factor(habitat)for	-0.0124746	0.0461532	-0.2703	0.7899
factor(habitat)gra	0.0086361	0.0434242	0.1989	0.8445
factor(habitat)mou	0.0615649	0.0533889	1.1531	0.2632
factor(habitat)tun	-0.0207286	0.0870846	-0.2380	0.8144
factor(habitat)woo	0.0502388	0.0432959	1.1604	0.2603

Residual standard error: 0.3394 on 19 degrees of freedom

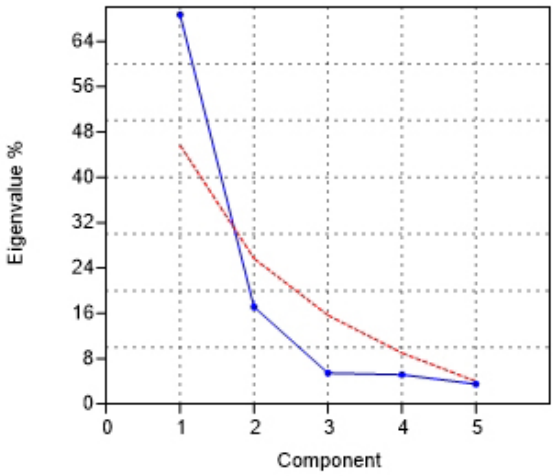
Multiple R-squared: 0.1881, Adjusted R-squared: -0.02559

F-statistic: 0.8802 on 5 and 19 DF, p-value: 0.5131

Appendix J: Eigenvalues associated with bg-PCA on calcaneus model with fossil specimens

1. Eigenvalues associated with bg-PCA on all extant calcanei and Trinil fossils (II), with broken stick model of eigenvalue distributions (I).

I

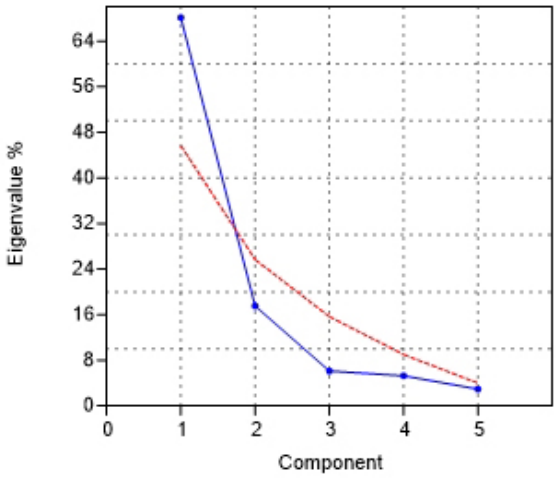


II

PC	Eigenvalue	% variance
1	0.00048	68.698
2	0.00012	17.134
3	3.82E-05	5.4641
4	3.62E-05	5.1828
5	2.46E-05	3.5205

2. Eigenvalues associated with bg-PCA on all extant calcanei and *Axis lydekkeri* fossils (II), with broken stick model of eigenvalue distributions (I).

I

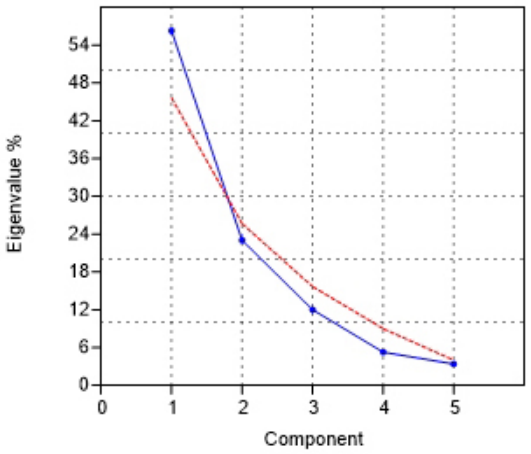


II

PC	Eigenvalue	% variance
1	0.000476	68.12
2	0.000123	17.527
3	4.28E-05	6.1197
4	3.70E-05	5.2842
5	2.06E-05	2.9492

3. Eigenvalues associated with bg-PCA on all extant calcanei and *Cervus kendengensis* fossils from the Kedung Brubus faunal unit (II), with broken stick model of eigenvalue distributions (I).

I

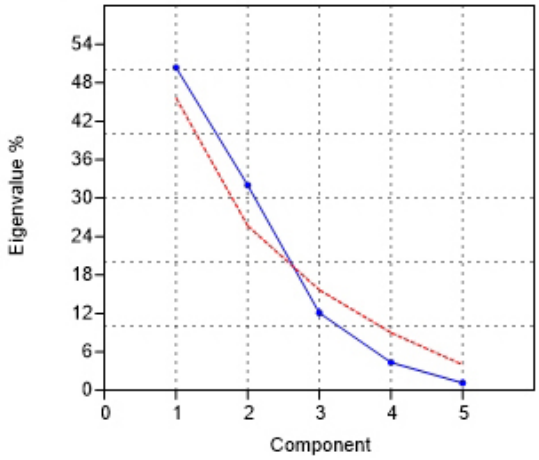


II

PC	Eigenvalue	% variance
1	0.000386	56.294
2	0.000158	23.036
3	8.23E-05	12.009
4	3.62E-05	5.2731
5	2.32E-05	3.3881

4. Eigenvalues associated with bg-PCA on all extant calcanei and Sangiran fossils (II), with broken stick model of eigenvalue distributions (I).

I



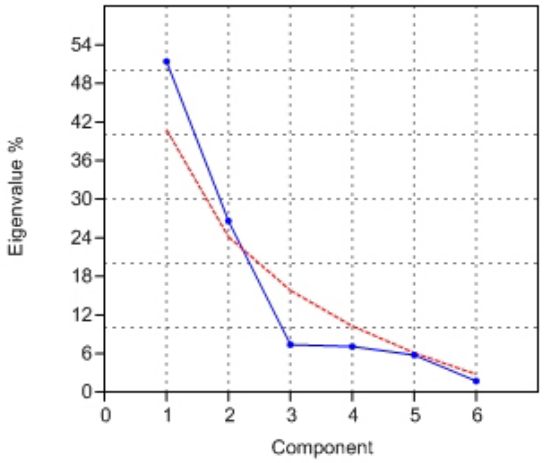
II

PC	Eigenvalue	% variance
1	0.000390727	50.371
2	0.000248426	32.026
3	9.38E-05	12.091
4	3.38E-05	4.356
5	8.96E-06	1.1556

Appendix K: Eigenvalues associated with bg-PCA on intermediate phalanx model with fossil specimens

1. Eigenvalues associated with bg-PCA on all extant phalanges and fossils from Trinil (II), with broken stick model of eigenvalue distributions (I).

I

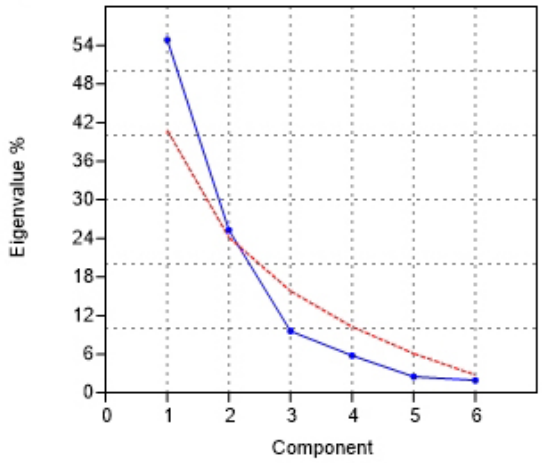


II

PC	Eigenvalue	% variance
1	0.001465	51.414
2	0.000758	26.615
3	0.00021	7.3793
4	0.000202	7.0912
5	0.000164	5.7684
6	4.94E-05	1.7323

2. Eigenvalues associated with bg-PCA on all extant phalanges and *Axis lydekkeri* fossils (II), with broken stick model of eigenvalue distributions (I).

I

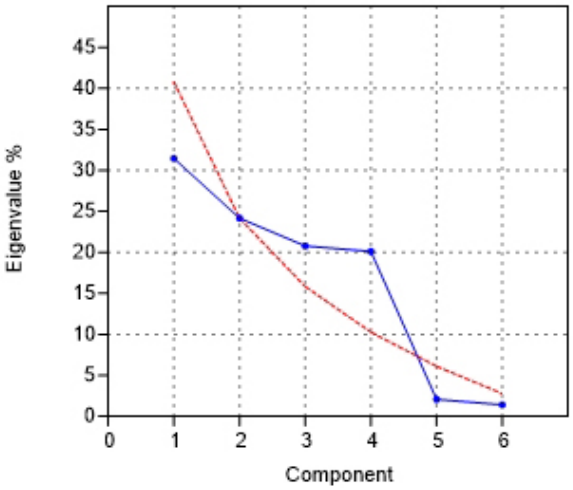


II

PC	Eigenvalue	% variance
1	0.00145	54.857
2	0.000669	25.291
3	0.000254	9.5982
4	0.000153	5.792
5	6.65E-05	2.515
6	5.15E-05	1.9469

3. Eigenvalues associated with bg-PCA on all extant phalanges and *Cervus kendengensis* fossils from the Kedung Brubus faunal unit (II), with broken stick model of eigenvalue distributions (I).

I

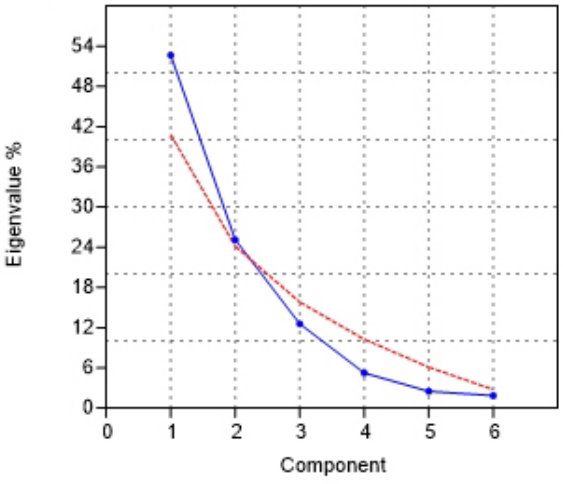


II

PC	Eigenvalue	% variance
1	0.00103959	31.457
2	0.000798581	24.164
3	0.000686808	20.782
4	0.000664922	20.12
5	6.86E-05	2.0744
6	4.64E-05	1.4033

4. Eigenvalues associated with bg-PCA on all extant phalanges and fossils from Sangiran (II), with broken stick model of eigenvalue distributions (I).

I

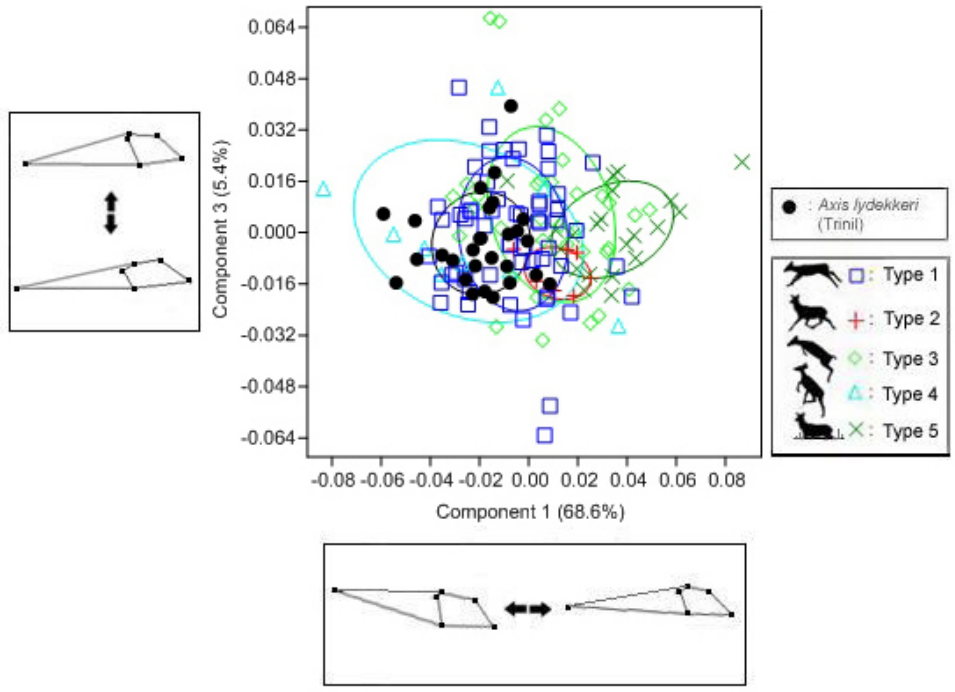


II

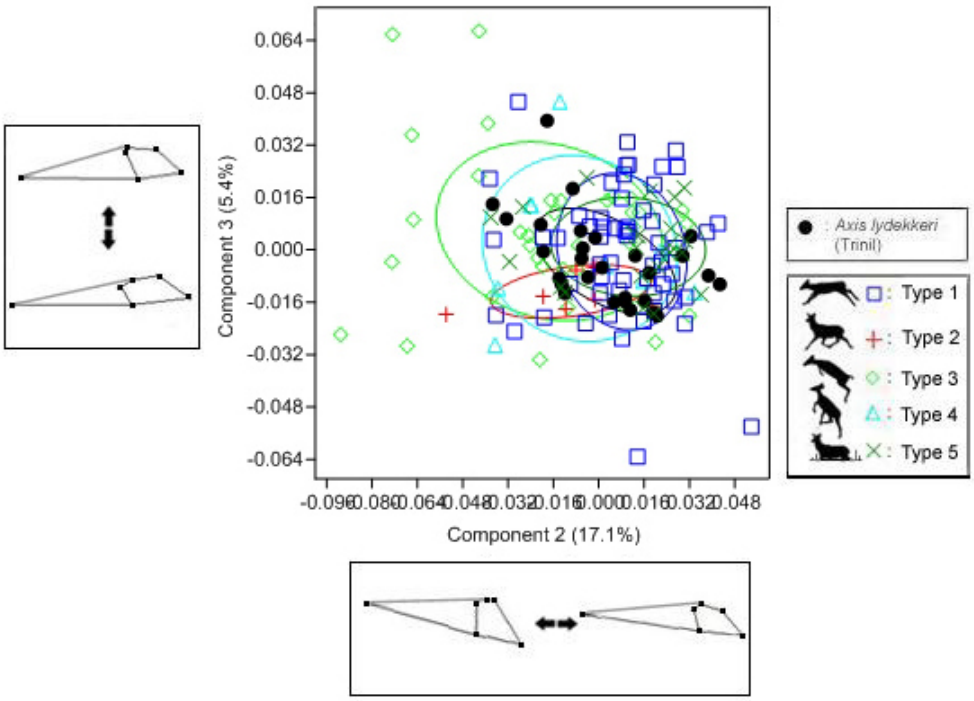
PC	Eigenvalue	% variance
1	0.00136231	52.671
2	0.000649884	25.126
3	0.000325457	12.583
4	0.000135626	5.2437
5	6.49E-05	2.5078
6	4.83E-05	1.8684

Appendix L: bg-PCA scatterplots of PC3 and PC4 of the fossil calcaneus analyses, with associated results of Krukal-Wallis test

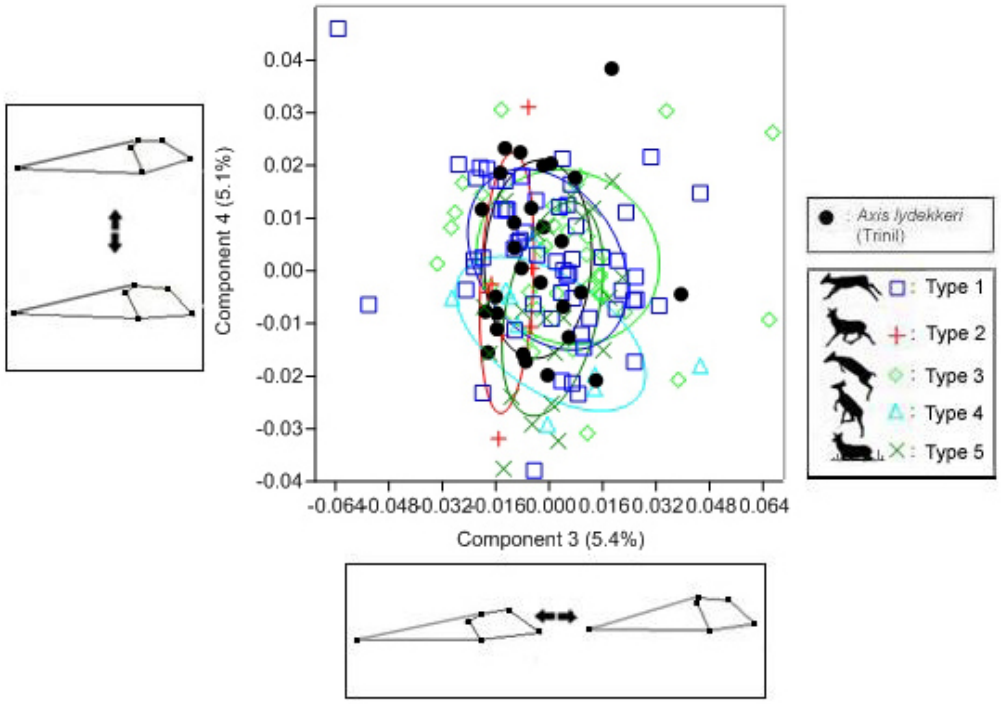
1. PC1 and PC3 scatterplot of a between groups PCA of all extant calcanei and fossil calcanei from Trinil ordered by habitat/locomotor strategy with 50% confidence intervals.



2. PC2 and PC3 scatterplot of a between groups PCA of all extant calcanei and fossil calcanei from Trinil ordered by habitat/locomotor strategy with 50% confidence intervals.



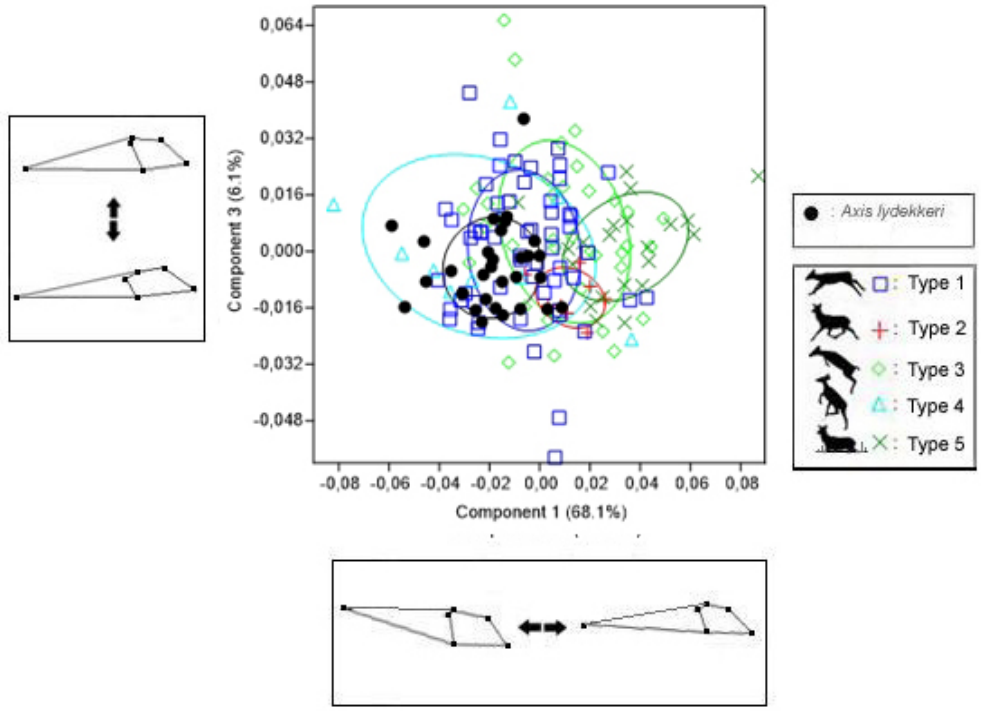
3. PC3 and PC4 scatterplot of a between groups PCA of all extant calcanei and fossil calcanei from Trinil ordered by habitat/locomotor strategy with 50% confidence intervals.



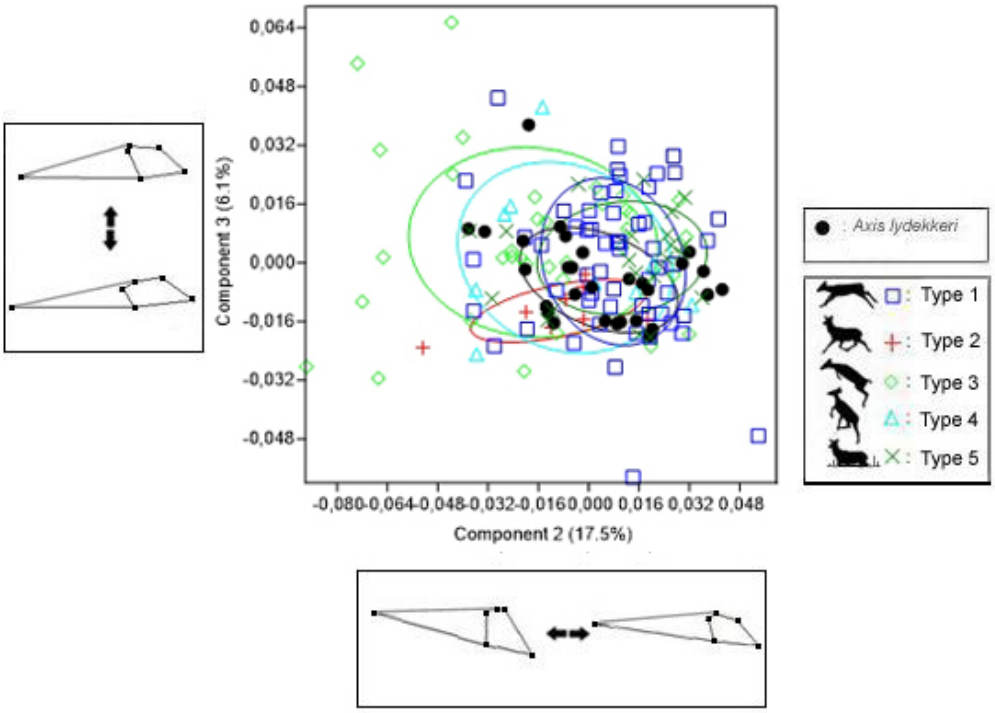
4. p-values of pairwise comparisons of a Kruskal-Wallis test for PC3 and PC4 of the bg- PCA on all extant calcaneus specimens and fossils from Trinil, with significant values ($p<0.05$) in bold. (TRIN=Trinil)

PC3	Type 3	Type 2	Type 4	Type 1	TRIN	Type 5
Type 3	-	**0.007621**	0.4153	0.2776	**0.03259**	0.4984
Type 2	**0.007621**	-	0.07505	**0.03692**	0.06497	**0.00431**
Type 4	0.4153	0.07505	-	0.8518	0.6839	0.6838
Type 1	0.2776	**0.03692**	0.8518	-	0.2843	0.8925
TRIN	**0.03259**	0.06497	0.6839	0.2843	-	0.1486
Type 5	0.4984	**0.00431**	0.6838	0.8925	0.1486	-
PC4	Type 3	Type 2	Type 4	Type 1	TRIN	Type 5
Type 3	-	0.4082	**0.004768**	0.8906	0.7767	**0.03737**
Type 2	0.4082	-	0.229	0.3328	0.6343	0.5747
Type 4	**0.004768**	0.229	-	**0.007541**	**0.02458**	0.469
Type 1	0.8906	0.3328	**0.007541**	-	0.8922	**0.02287**
TRIN	0.7767	0.6343	**0.02458**	0.8922	-	0.07378
Type 5	**0.03737**	0.5747	0.469	**0.02287**	0.07378	-

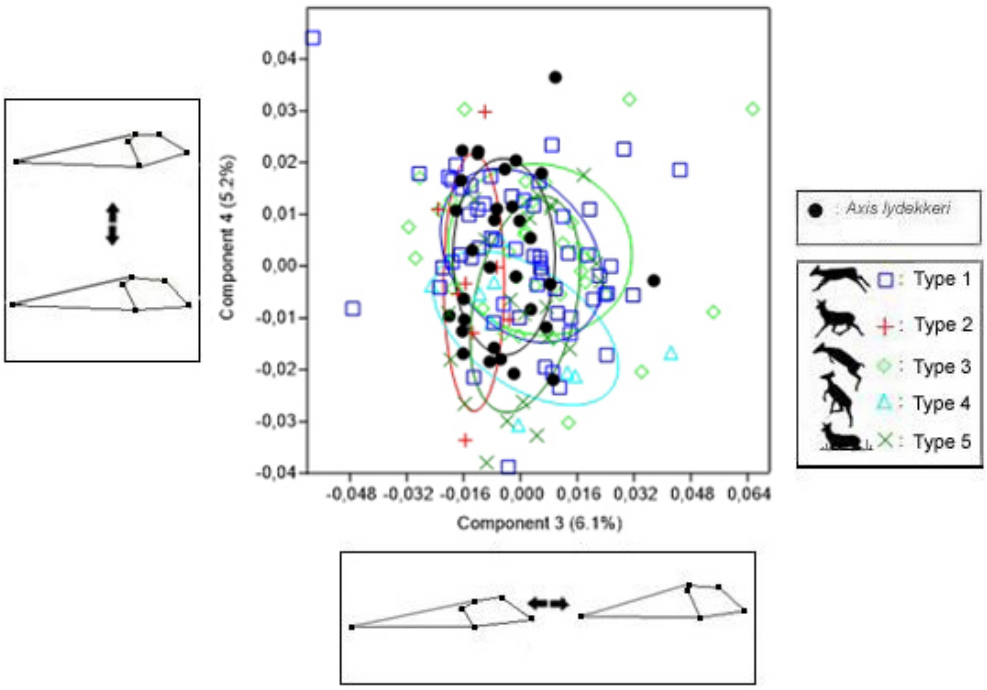
5. PC1 and PC3 scatterplot of a between groups PCA of all extant calcanei and fossil *Axis lydekkeri* calcanei ordered by habitat/locomotor strategy with 50% confidence intervals.



6. PC2 and PC3 scatterplot of a between groups PCA of all extant calcanei and fossil *Axis lydekkeri* calcanei ordered by habitat/locomotor strategy with 50% confidence intervals.



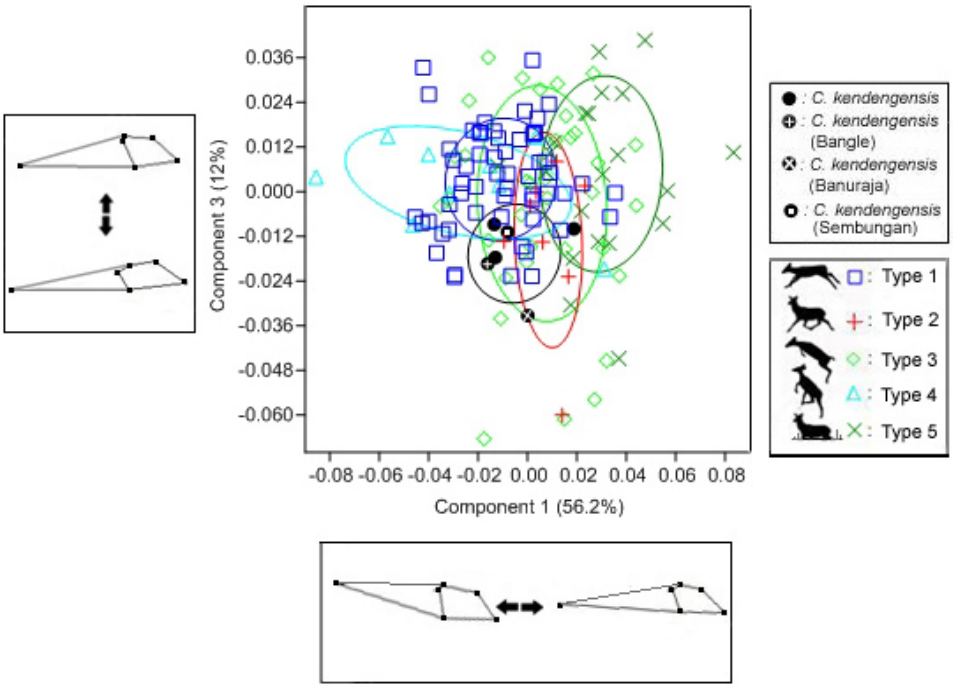
7. PC3 and PC4 scatterplot of a between groups PCA of all extant calcanei and fossil *Axis lydekkeri* calcanei ordered by habitat/locomotor strategy with 50% confidence intervals.



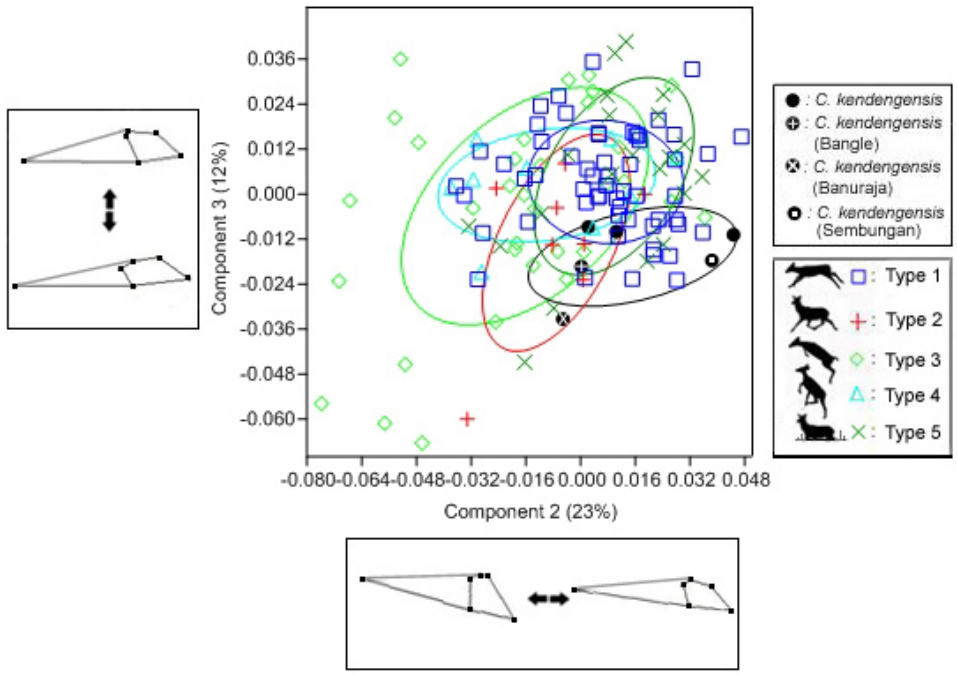
8. p-values of pairwise comparisons of a Kruskal-Wallis test for PC3 and PC4 of the bg- PCA on all extant calcaneus specimens and *Axis lydekkeri* fossils (ALY), with significant values ($p<0.05$) in bold.

PC3	Type 3	Type 2	Type 4	Type 1	ALY	Type 5
Type 3	-	**0.009161**	0.3671	0.3807	**0.01056**	0.5312
Type 2	**0.009161**	-	0.0606	**0.02109**	0.07326	**0.006766**
Type 4	0.3671	0.0606	-	0.9702	0.3818	0.7173
Type 1	0.3807	**0.02109**	0.9702	-	0.1061	0.982
ALY	**0.01056**	0.07326	0.3818	0.1061	-	0.06485
Type 5	0.5312	**0.006766**	0.7173	0.982	0.06485	-
PC4	Type 3	Type 2	Type 4	Type 1	ALY	Type 5
Type 3	-	0.2419	**0.004768**	0.7907	0.719	**0.04058**
Type 2	0.2419	-	0.2685	0.2765	0.5428	0.7511
Type 4	**0.004768**	0.2685	-	**0.007131**	**0.02543**	0.4153
Type 1	0.7907	0.2765	**0.007131**	-	0.8203	**0.03233**
ALY	0.719	0.5428	**0.02543**	0.8203	-	0.1008
Type 5	**0.04058**	0.7511	0.4153	**0.03233**	0.1008	-

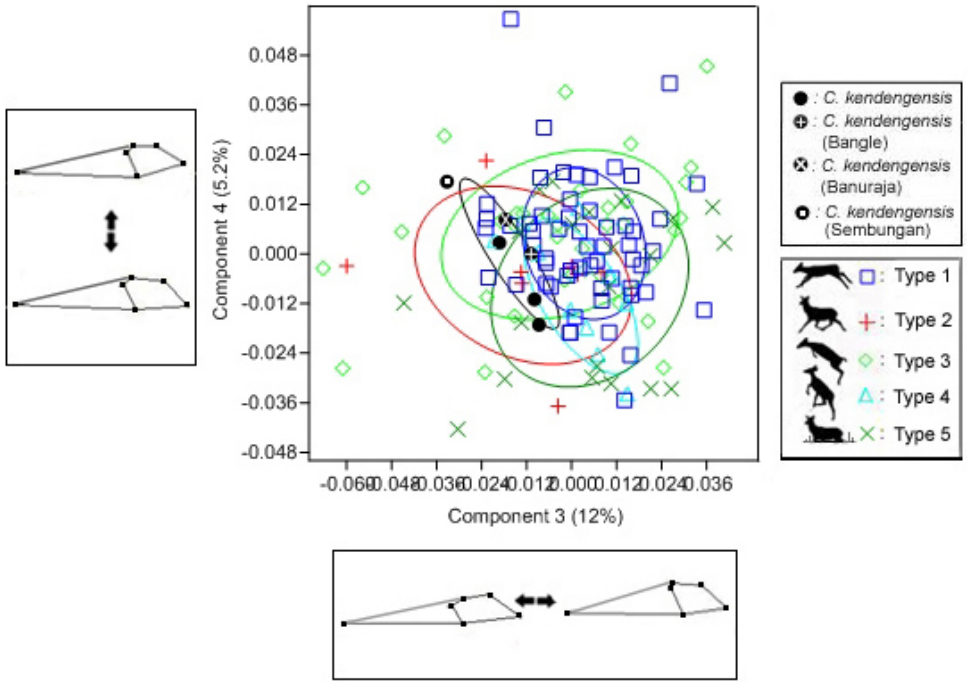
9. PC1 and PC3 scatterplot of a between groups PCA of all extant calcanei and fossil *Cervus kendengensis* calcanei ordered by habitat/locomotor strategy with 50% confidence intervals.



10. PC2 and PC3 scatterplot of a between groups PCA of all extant calcanei and fossil *Cervus kendengensis* calcanei ordered by habitat/locomotor strategy with 50% confidence intervals.



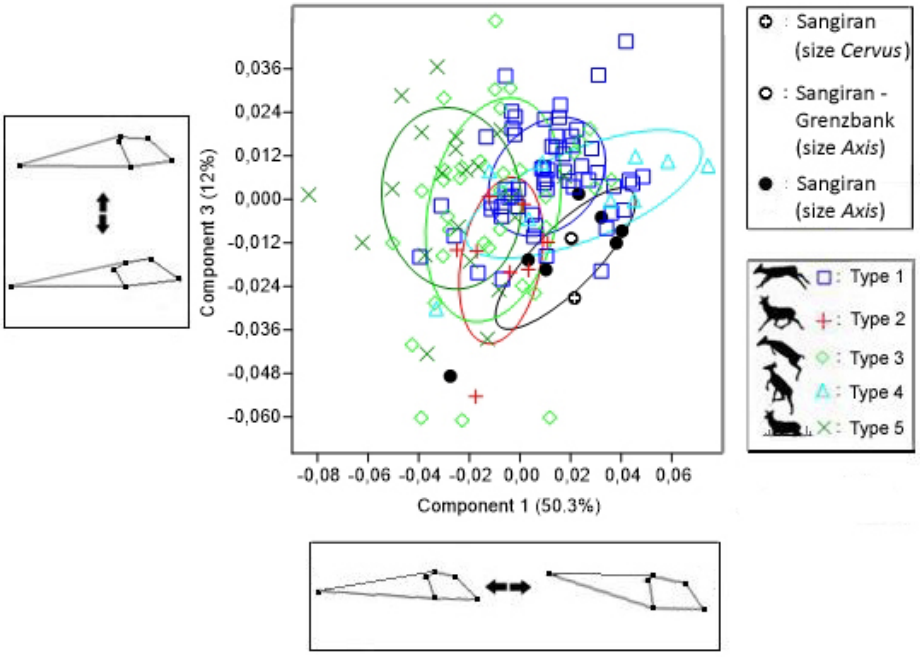
11. PC3 and PC4 scatterplot of a between groups PCA of all extant calcanei and fossil *Cervus kendengensis* calcanei ordered by habitat/locomotor strategy with 50% confidence intervals.



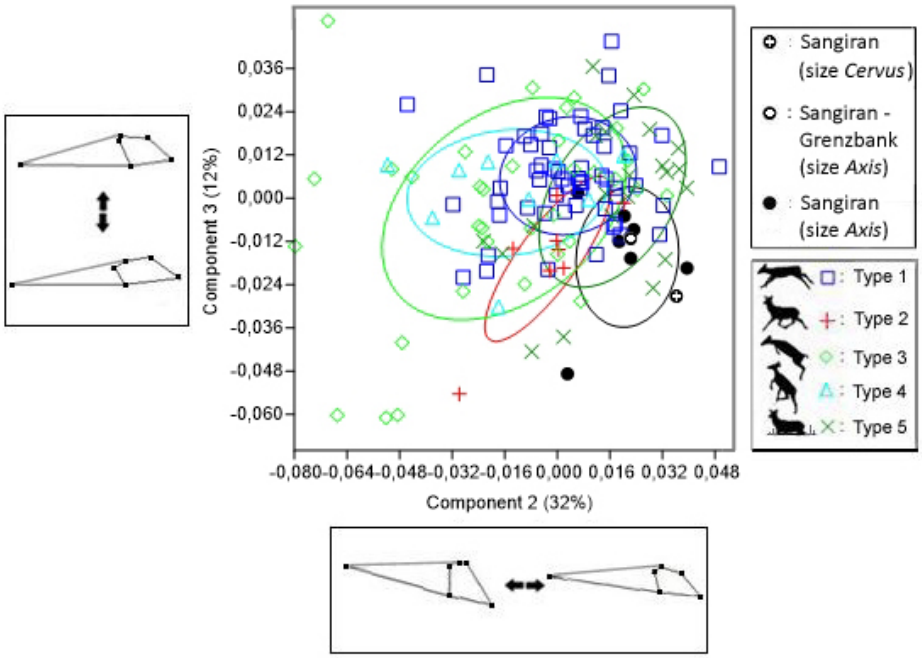
12. p-values of pairwise comparisons of a Kruskal-Wallis test for PC3 and PC4 of the bg- PCA on all extant calcaneus specimens and and *Cervus kendengensis* fossils (CKE), with significant values (p<0.05) in bold.

PC3	Type 3	CKE	Type 2	Type 4	Type 1	Type 5
Type 3	-	0.07362	0.2546	0.6416	0.4166	0.294
CKE	0.07362	-	0.4014	**0.01569**	**0.001637**	**0.01551**
Type 2	0.2546	0.4014	-	0.0606	**0.03183**	0.05393
Type 4	0.6416	**0.01569**	0.0606	-	0.9553	0.6186
Type 1	0.4166	**0.001637**	**0.03183**	0.9553	-	0.5505
Type 5	0.294	**0.01551**	0.05393	0.6186	0.5505	-
PC4	Type 3	CKE	Type 2	Type 4	Type 1	Type 5
Type 3	-	0.472	0.1382	**0.01704**	0.3426	**0.04226**
CKE	0.472	-	0.4777	0.2159	0.7698	0.466
Type 2	0.1382	0.4777	-	0.4705	0.1978	0.9417
Type 4	**0.01704**	0.2159	0.4705	-	**0.03316**	0.5871
Type 1	0.3426	0.7698	0.1978	**0.03316**	-	0.1122
Type 5	**0.04226**	0.466	0.9417	0.5871	0.1122	-

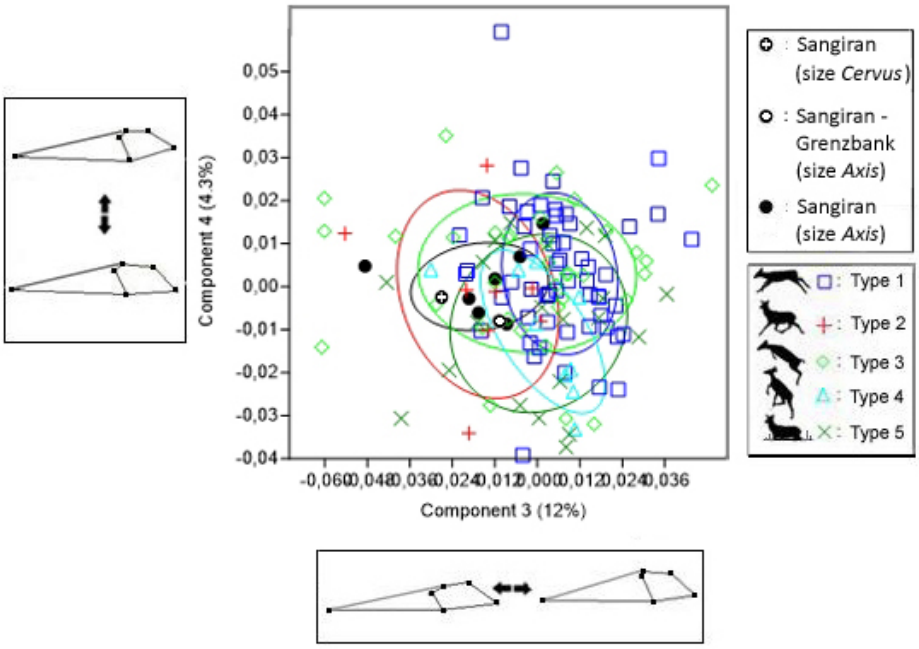
13. PC1 and PC3 scatterplot of a between groups PCA of all extant calcanei and fossil calcanei from Sangiran ordered by habitat/locomotor strategy with 50% confidence intervals.



14. PC2 and PC3 scatterplot of a between groups PCA of all extant calcanei and fossil calcanei from Sangiran ordered by habitat/locomotor strategy with 50% confidence intervals.



15. PC3 and PC4 scatterplot of a between groups PCA of all extant calcanei and fossil calcanei from Sangiran ordered by habitat/locomotor strategy with 50% confidence intervals.

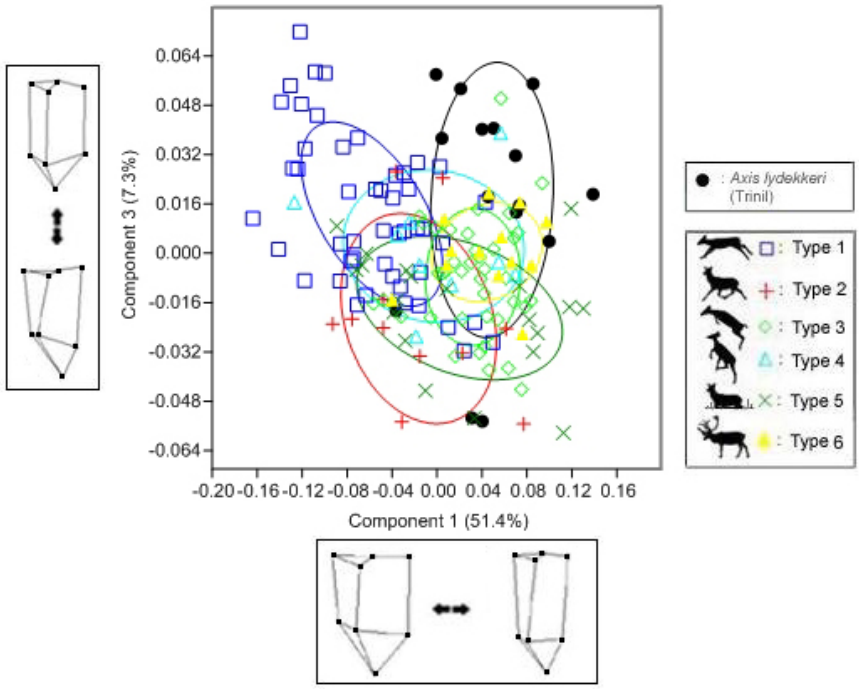


16. p-values of pairwise comparisons of a Kruskal-Wallis test for PC3 and PC4 of the bg- PCA on all extant calcaneus specimens and Sangiran *fossils, with significant values (p<0.05) in bold.*

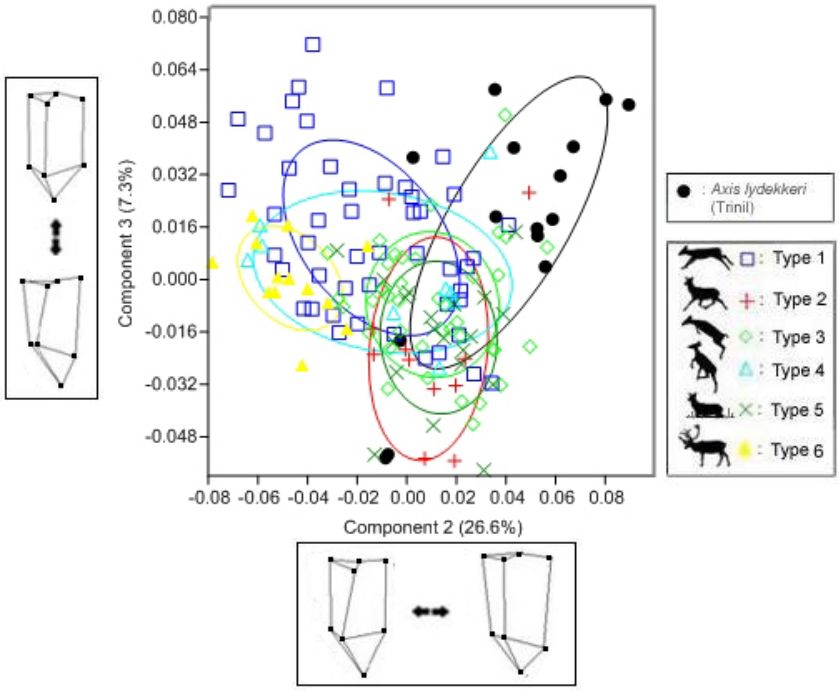
PC3	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5
Sangiran	-	**0.000138**	0.8099	**0.03367**	**0.01342**	**0.021**
Type 1	**0.000138**	-	**0.000616**	0.1168	0.6404	0.3383
Type 2	0.8099	**0.000616**	-	**0.04411**	**0.0184**	**0.0299**
Type 3	**0.03367**	0.1168	**0.04411**	-	0.5804	0.6722
Type 4	**0.01342**	0.6404	**0.0184**	0.5804	-	0.892
Type 5	**0.021**	0.3383	**0.0299**	0.6722	0.892	-
PC4	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5
Sangiran	-	0.5252	0.8099	0.3827	0.1853	0.2774
Type 1	0.5252	-	0.5558	0.7845	**0.0288**	**0.01406**
Type 2	0.8099	0.5558	-	0.3412	0.4134	0.4208
Type 3	0.3827	0.7845	0.3412	-	**0.03131**	**0.02135**
Type 4	0.1853	**0.0288**	0.4134	**0.03131**	-	0.7514
Type 5	0.2774	**0.01406**	0.4208	**0.02135**	0.7514	-

Appendix M: bg-PCA scatterplots of PC3 and PC4 of the fossil intermediate phalanx analyses, with associated results of Krukal-Wallis test

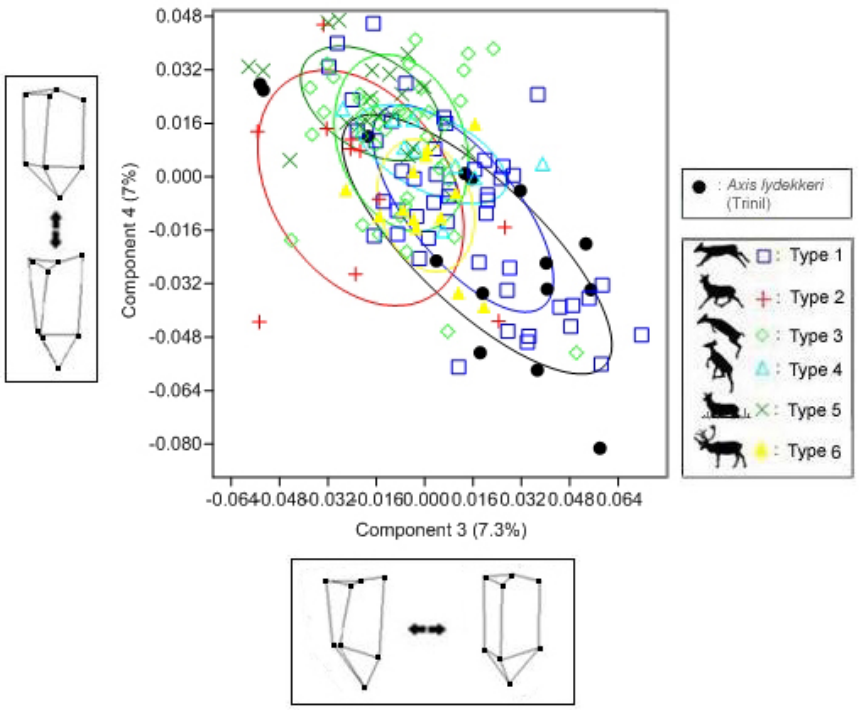
1. PC1 and PC3 scatterplot of a between groups PCA of all extant intermediate phalanges and fossil Phalanges from Trinil ordered by habitat/locomotor strategy with 50% confidence intervals.



2. PC2 and PC3 scatterplot of a between groups PCA of all extant intermediate phalanges and fossil Phalanges from Trinil ordered by habitat/locomotor strategy with 50% confidence intervals.



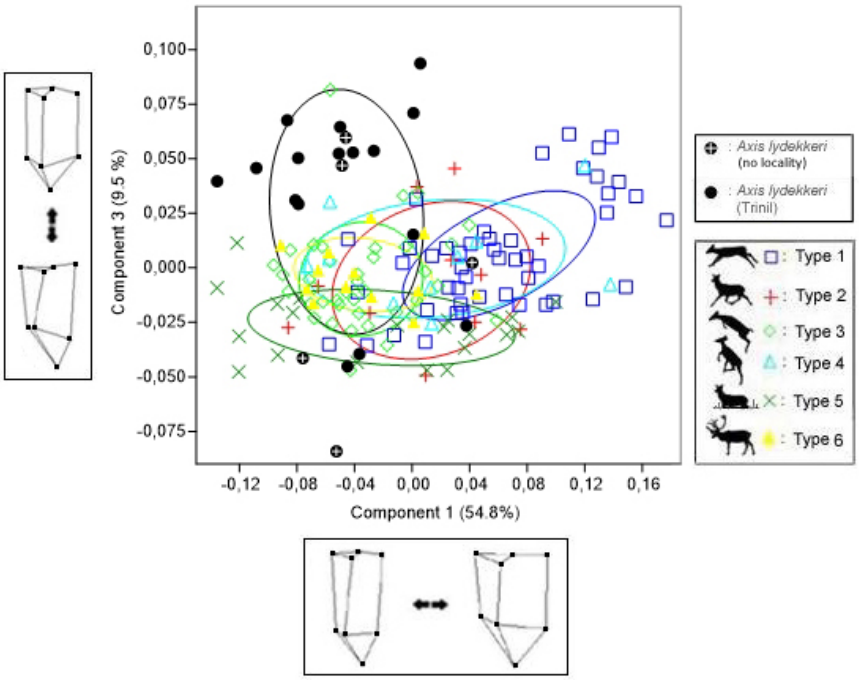
3. PC3 and PC4 scatterplot of a between groups PCA of all extant intermediate phalanges and fossil Phalanges from Trinil ordered by habitat/locomotor strategy with 50% confidence intervals.



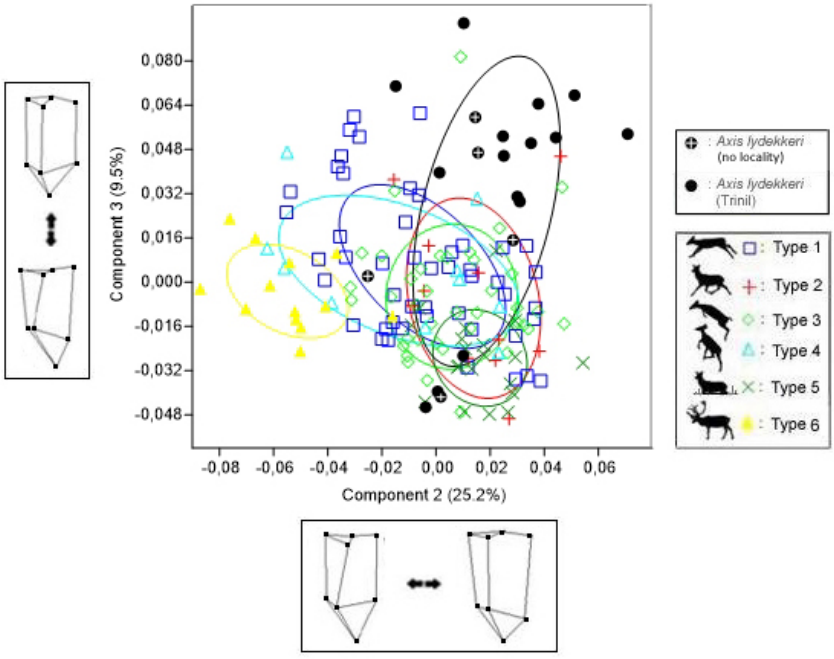
4. p-values of pairwise comparisons of a Kruskal-Wallis test for PC3 and PC4 of the bg- PCA on all extant intermediate phalanx specimens and Trinil fossils, with significant values ($p<0.05$) in bold.

PC3	Trinil	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Trinil	-	0.2905	**0.008123**	**0.001652**	0.08377	**0.001154**	**0.02703**
Type 1	0.2905	-	**0.000477**	**0.00016**	0.2417	**1.81E-05**	0.09962
Type 2	**0.008123**	**0.000477**	-	**0.03225**	**0.0334**	0.2739	**0.02385**
Type 3	**0.001652**	**0.00016**	**0.03225**	-	0.1672	0.09805	0.08067
Type 4	0.08377	0.2417	**0.0334**	0.1672	-	**0.01519**	0.8938
Type 5	**0.001154**	**1.81E-05**	0.2739	0.09805	**0.01519**	-	**0.002675**
Type 6	**0.02703**	0.09962	**0.02385**	0.08067	0.8938	**0.002675**	-
PC4	Trinil	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Trinil	-	0.2553	0.2129	**0.000975**	**0.02004**	**0.000103**	0.3109
Type 1	0.2553	-	0.442	**0.00029**	**0.03111**	**3.32E-06**	0.9789
Type 2	0.2129	0.442	-	0.05584	0.4033	**0.004683**	0.4869
Type 3	**0.000975**	**0.00029**	0.05584	-	0.2506	0.09336	**0.003012**
Type 4	**0.02004**	**0.03111**	0.4033	0.2506	-	**0.01519**	**0.02318**
Type 5	**0.000103**	**3.32E-06**	**0.004683**	0.09336	**0.01519**	-	**2.89E-05**
Type 6	0.3109	0.9789	0.4869	**0.003012**	**0.02318**	**2.89E-05**	-

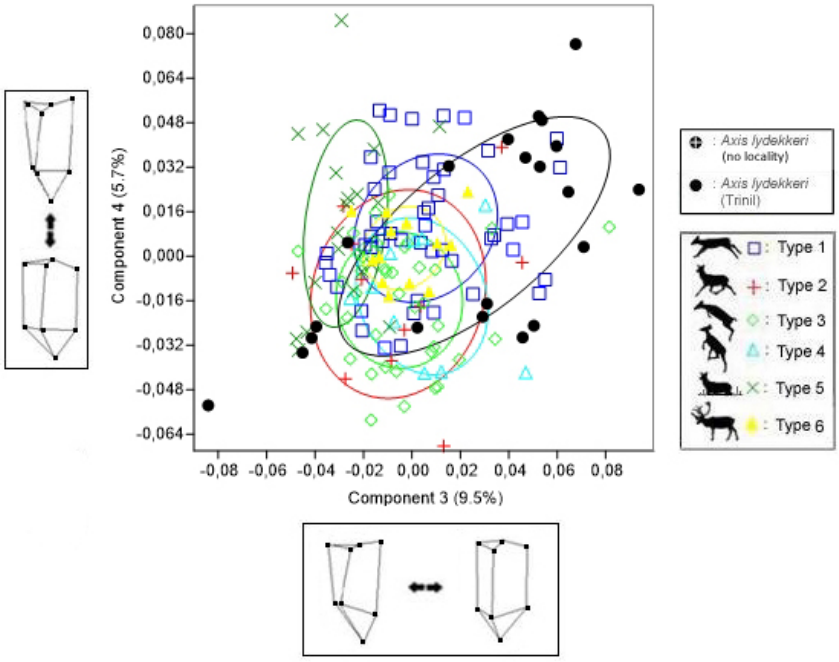
5. PC1 and PC3 scatterplot of a between groups PCA of all extant intermediate phalanges and *Axis lydekkeri* phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.



6. PC2 and PC3 scatterplot of a between groups PCA of all extant intermediate phalanges and *Axis lydekkeri* phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.



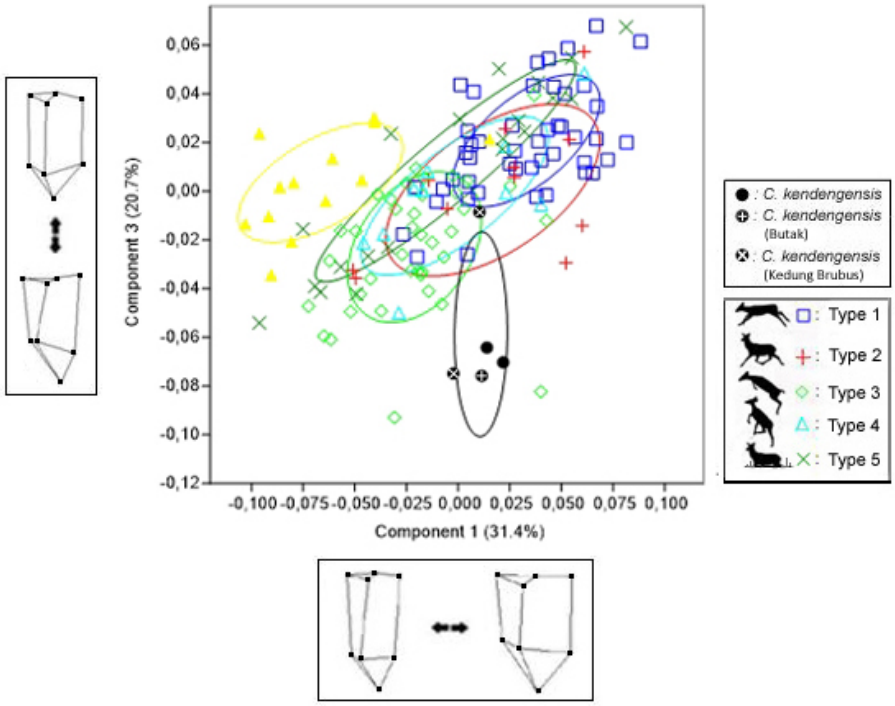
7. PC3 and PC4 scatterplot of a between groups PCA of all extant intermediate phalanges and *Axis lydekkeri* phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.



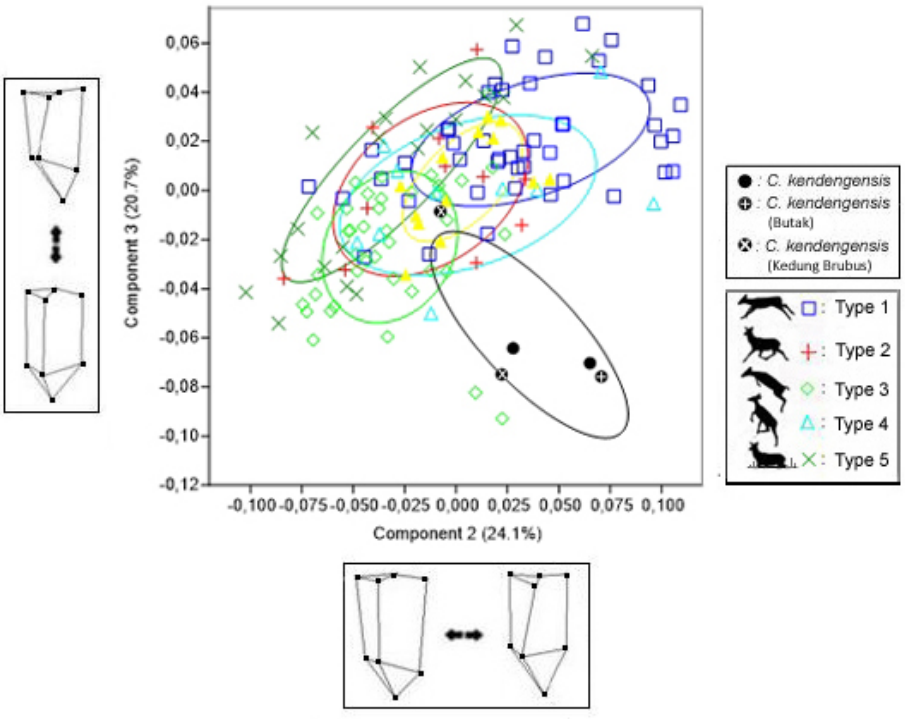
8. p-values of pairwise comparisons of a Kruskal-Wallis test for PC3 and PC4 of the bg- PCA on all extant intermediate phalanx specimens and *Axis lydekkeri* fossils (ALY), with significant values (p<0.05) in bold.

PC3	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	ALY
Type 1	-	0.1889	**0.03691**	0.9262	**1.07E-06**	0.3552	**0.01992**
Type 2	0.1889	-	0.7967	0.3072	**0.0302**	0.6021	**0.0291**
Type 3	**0.03691**	0.7967	-	0.1845	**4.60E-05**	0.4343	**0.003572**
Type 4	0.9262	0.3072	0.1845	-	**0.000284**	0.4382	0.07948
Type 5	**1.07E-06**	**0.0302**	**4.60E-05**	**0.000284**	-	**0.000118**	**0.000604**
Type 6	0.3552	0.6021	0.4343	0.4382	**0.000118**	-	**0.02125**
ALY	**0.01992**	**0.0291**	**0.003572**	0.07948	**0.000604**	**0.02125**	-
PC4	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	ALY
Type 1	-	**0.01623**	**3.65E-06**	**0.009215**	0.9732	0.3461	0.6434
Type 2	**0.01623**	-	0.9254	0.9719	**0.04987**	0.1178	0.1421
Type 3	**3.65E-06**	0.9254	-	0.8719	**0.001325**	**0.005634**	**0.01773**
Type 4	**0.009215**	0.9719	0.8719	-	**0.0263**	0.07715	0.1449
Type 5	0.9732	**0.04987**	**0.001325**	**0.0263**	-	0.4071	0.8654
Type 6	0.3461	0.1178	**0.005634**	0.07715	0.4071	-	0.8316
ALY	0.6434	0.1421	**0.01773**	0.1449	0.8654	0.8316	-

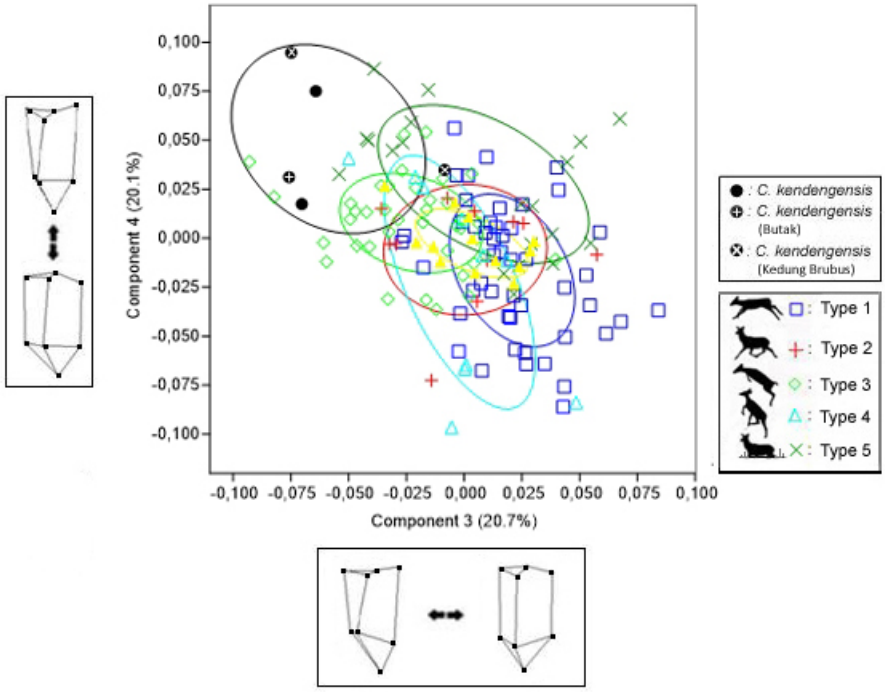
9. PC1 and PC3 scatterplot of a between groups PCA of all extant intermediate phalanges and *Cervus kendengensis* phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.



10. PC2 and PC3 scatterplot of a between groups PCA of all extant intermediate phalanges and *Cervus kendengensis* phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.



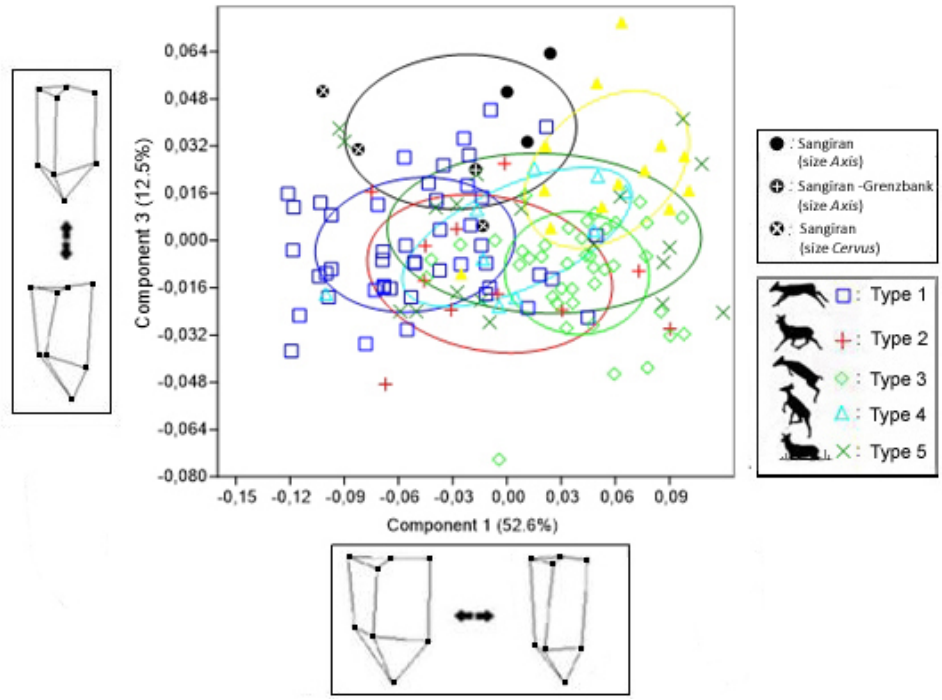
11. PC3 and PC4 scatterplot of a between groups PCA of all extant intermediate phalanges and *Cervus kendengensis* phalanges ordered by habitat/locomotor strategy with 50% confidence intervals.



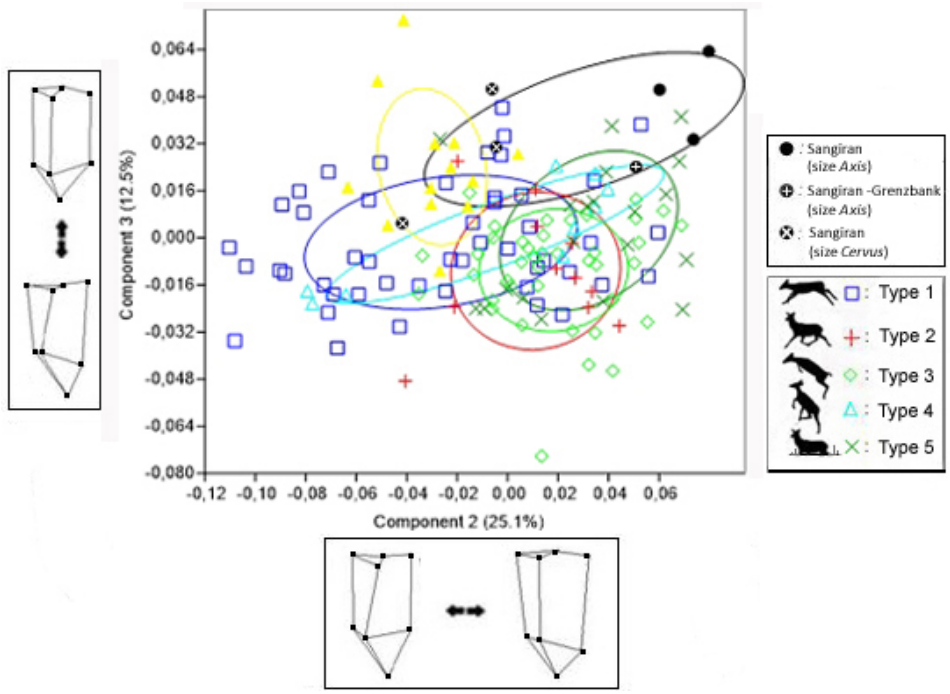
12. p-values of pairwise comparisons of a Kruskal-Wallis test for PC3 and PC4 of the bg- PCA on all extant intermediate phalanx specimens and *Cervus kendegensis* fossils (CKE), with significant values (p<0.05) in bold.

PC3	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	CKE
Type 1	-	**0.02585**	**4.31E-11**	**0.008676**	0.5492	**0.03533**	**0.000393**
Type 2	**0.02585**	-	**0.0169**	0.8053	0.4957	0.6851	**0.009171**
Type 3	**4.31E-11**	**0.0169**	-	**0.03832**	**0.005202**	**0.002342**	**0.01982**
Type 4	**0.008676**	0.8053	**0.03832**	-	0.4157	0.4382	**0.008458**
Type 5	0.5492	0.4957	**0.005202**	0.4157	-	0.5432	**0.004812**
Type 6	**0.03533**	0.6851	**0.002342**	0.4382	0.5432	-	**0.005779**
CKE	**0.000393**	**0.009171**	**0.01982**	**0.008458**	**0.004812**	**0.005779**	-
PC4	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	CKE
Type 1	-	0.2631	**0.000417**	0.8129	**6.97E-05**	0.2209	**0.001474**
Type 2	0.2631	-	0.1819	0.6985	**0.01967**	0.7281	**0.003224**
Type 3	**0.000417**	0.1819	-	0.161	**0.03811**	0.07588	**0.004947**
Type 4	0.8129	0.6985	0.161	-	**0.01462**	0.6869	**0.02346**
Type 5	**6.97E-05**	**0.01967**	**0.03811**	**0.01462**	-	**0.01581**	0.2923
Type 6	0.2209	0.7281	0.07588	0.6869	**0.01581**	-	**0.003105**
CKE	**0.001474**	**0.003224**	**0.004947**	**0.02346**	0.2923	**0.003105**	-

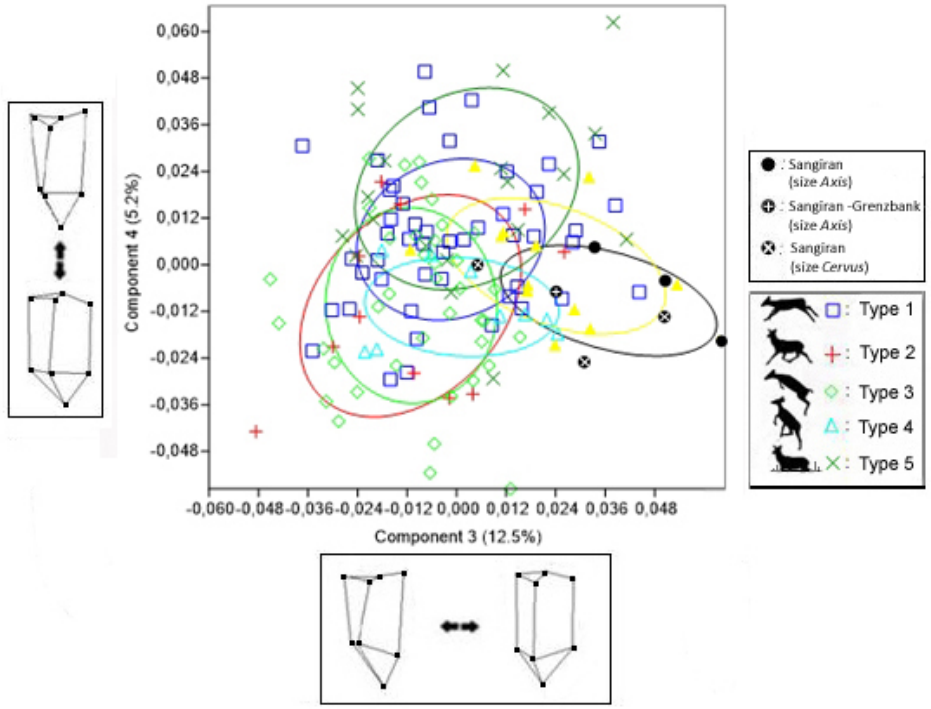
13. PC1 and PC3 scatterplot of a between groups PCA of all extant intermediate phalanges and Sangiran phalanges, ordered by habitat/locomotor strategy with 50% confidence intervals.



14. PC2 and PC3 scatterplot of a between groups PCA of all extant intermediate phalanges and Sangiran phalanges, ordered by habitat/locomotor strategy with 50% confidence intervals.



15. PC3 and PC4 scatterplot of a between groups PCA of all extant intermediate phalanges and Sangiran phalanges, ordered by habitat/locomotor strategy with 50% confidence intervals.



16. p-values of pairwise comparisons of a Kruskal-Wallis test for PC3 and PC4 of the bg- PCA on all extant intermediate phalanx specimens and Sangiran fossils, with significant values ($p<0.05$) in bold.

PC3	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Sangiran	-	**0.000469**	**0.001525**	**7.52E-05**	**0.005921**	**0.006167**	0.1538
Type 1	**0.000469**	-	0.17	0.1181	0.751	0.6618	**0.000698**
Type 2	**0.001525**	0.17	-	0.6552	0.1965	0.2079	**0.001177**
Type 3	**7.52E-05**	0.1181	0.6552	-	0.1309	0.05279	**3.83E-06**
Type 4	**0.005921**	0.751	0.1965	0.1309	-	0.9812	**0.01943**
Type 5	**0.006167**	0.6618	0.2079	0.05279	0.9812	-	**0.01931**
Type 6	0.1538	**0.000698**	**0.001177**	**3.83E-06**	**0.01943**	**0.01931**	-
PC4	Sangiran	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Sangiran	-	**0.01588**	0.8563	0.9167	0.8323	**0.001772**	0.2048
Type 1	**0.01588**	-	**0.03642**	**0.000363**	**0.003024**	**0.01953**	0.1563
Type 2	0.8563	**0.03642**	-	0.9361	0.9394	**0.003607**	0.2024
Type 3	0.9167	**0.000363**	0.9361	-	0.9691	**2.38E-05**	0.1339
Type 4	0.8323	**0.003024**	0.9394	0.9691	-	**0.000531**	**0.04514**
Type 5	**0.001772**	**0.01953**	**0.003607**	**2.38E-05**	**0.000531**	-	**0.007559**
Type 6	0.2048	0.1563	0.2024	0.1339	**0.04514**	**0.007559**	-